Novel methods for quantifying movement behavior of free-ranging fish from telemetry data

by

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Statements and declarations

Declaration of Originality

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The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University. All research conducted for this thesis was approved by the University of Tasmania Animal Ethics Committee (Permit No. A0011590).

Kilian Michael Stehfest

Hobart, 3rd of April, 2013

Statement of Co-Authorship

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Abstract

In recent decades, technological progress in the field of biotelemetry has allowed the collection of vast amounts of data on the movement of free-ranging marine animals and recently there have been great advances in analysing data from tags that allow the observation of complete animal tracks. One of the most common and low-cost tools for tracking marine animals, however, are automated acoustic arrays, which often do not record complete tracks but provide presence/absence data for tagged animals at fixed locations. The development of quantitative methods for analysing these data has lagged behind the technological advances in the field.

This thesis applies novel methods for quantifying the movement behaviour of highly mobile free-ranging teleosts and elamsobranchs using automated acoustic tracking data and answers ecological questions of management relevance for tropical tuna (Yellowfin tuna *Thunnus albacares*) and a temperate shark species (Broadnose sevengill shark *Notorynchus cepedianus*). Additionally, pop-up satellite archival tag (PSAT) data are analysed for the temperate shark species, to put the findings of the acoustic tracking data analysis into the context of the animals' large-scale movement behaviour.

The two acoustic datasets represent two different types of common receiver array designs: For the tuna study, individual receivers were deployed at ecologically significant locations (fish aggregating devices, FADs) to determine the residency at and movement between these

locations. For the shark study, receivers were deployed as multiple curtains between opposite shorelines to detect passes of animals through the curtains and determine general movement patterns within a coastal area.

Network analysis methods were applied to both datasets to quantify the co-occurrence of individuals at a given location and to determine the relative importance of each location to the animals. For the former, we adapted association indices from social network analysis to quantify temporally explicit joint occurrences of individuals. For the latter we treated the number of transitions between locations as a measure of the connectivity between them. The network analysis approach to the acoustic tracking data was well suited to the type of array used in the tuna study and was a considerable improvement over traditional measures of co-occurrence which often only include either the spatial or the temporal dimension, not both. It provided new insight into the temporal dynamics of tuna aggregations at FADs and how they may be linked to between-FAD movement. We observed large interannual variation in movement rates of tuna between FADs, and corresponding interannual variability in the mean number of spatio-temporal associates for each individual as well as the temporal stability of associations. When movement rates were high, associations within FAD aggregations decayed to randomness three times faster than when movement rates were lower. This raises the possibility that if FADs are sufficiently close for fish to perform frequent between-FAD movements, school mixing may be increased and cohesion reduced.

For the shark data, we compared results from the network analysis to a Markovian movement model estimated from counts of observed transitions. Specifically, we tested the suitability of the two methods for determining whether the differences in large-scale movement behaviour between males and females we established from the PSAT data are mirrored in their space-use during their coastal summer residency. Both spatial network analysis and Markov chain analysis showed differences in space-use between male and female broadnose sevengill sharks, however, rankings of the relative importance of geographic areas differed between the two approaches. This indicated that not only transitions but also residency periods, which are not accounted for by spatial network analysis, were important for identifying priority areas for the sharks.

Determining how animals interact and move within their environment has been a relatively understudied area, lacking in quantitative analytical methods. This thesis has applied various novel approaches which quantify both how individuals interact and use space, deepening our understanding of the two and the link between them.

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Chapter 1 - General Introduction

1.1 Movement ecology: Concepts and significance

Many applied questions in population dynamics and conservation biology have an explicit spatial dimension (Morales et al. 2010). This spatial dimension is fundamentally linked to the movement behavior of individuals (Patterson et al. 2008). As individuals move from one location to another, they influence not only their own chances of survival and reproduction and the distribution and genetic dispersal of their species (Bowler & Benton 2005), but also the structure and dynamics of the populations, communities and ecosystems they encounter (Nathan et al. 2008). Moreover, movement patterns are likely to play an important role in the response and adaptability of animal populations to perturbations such as overexploitation (Field et al. 2009), disease (Green et al. 2006), habitat loss (Green et al. 2006) or climate change (Drinkwater 2005).

Yet, movement is still a relatively poorly understood behavioral activity and most traditional models of population dynamics derive demographic parameters such as reproductive rates or predation risk as a function of overall population density, ignoring individual movement (Turchin 2003). This is partly due to the fact that the quantitative analysis of movement behavior as a formal discipline is relatively new (Turchin 1998) and only recently a unifying paradigm for the study of movement ecology has emerged (Nathan et al. 2008). Under this

movement ecology paradigm an organism's movement track is driven by 3 fundamental factors:

1) What is the motivation behind the movement? This question relates to the internal state of an organism and hence the goal of the movement such as finding food or a mate or escaping predation.
2) How is the movement performed? This question relates to the physical capacity of an animal to perform the movement required to reach the goal determined by the internal state.
3) When and to what destination is the movement performed? This question relates to the navigational and sensory capacity of an organism to detect times and/or locations when and/or towards which movement is performed to reach the goal of the movement.

All 3 factors are directly influenced by external environmental factors which can be chemical, physical and biological. Understanding how they interact both with each other and the external environmental factors to produce a movement track and determining the ecological consequences of the movement track is the overarching aim of movement ecological research (Nathan et al. 2008).

In the marine realm, where direct observation of the movement behavior of animals is extremely difficult, particularly for highly mobile species, quantifying all three aspects of an individual's movement track is almost impossible. While physiological and behavioral research can shed light on the motion, navigational and sensory capacities (Walker 1984, Wardle et al. 1989, Altringham & Block 1997, Montgomery et al. 2000, Donley & Shadwick 2003, Donley et al.

2005), determining the internal state of an individual directly in the field is impossible for most species. Hence, the majority of movement ecological research aims to determine the link between movement patterns and external factors, implicitly acknowledging internal state, movement and navigational capacity without quantifying them.

The main external factors which influence movement tracks can be divided into two categories (Revilla & Wiegand 2008):

(1) Habitats, which includes physical (Morrissey & Gruber 1993) and chemical (Brill 1994) as well as biological parameters such as distribution of prey (Sims et al. 2005)

(2) Interactions with conspecifics, which includes mating (Pratt & Carrier 2001), competition (Jones 1987) and schooling (Newlands et al. 2006).

Habitats in the marine realm exert their influence on movement patterns over a large range of temporal and spatial scales: From transient features such as eddies (Seki et al. 2002) to permanent physical structures such as reefs (Heupel et al. 2010) and from coastal areas with high habitat heterogeneity at fine spatial scales (Murchie et al. 2010) to the vast and relatively homogeneous open ocean habitat of pelagic predators (Block et al. 2011). Understanding the link between habitat and animal space-use patterns at multiple spatio-temporal scales is challenging but fundamental to developing effective management and conservation measures (Nathan et al. 2008) in the face of habitat loss and fragmentation, particularly in coastal areas (Speed et al. 2010).

Interactions with conspecifics are also likely to exert considerable influence on movement patterns of some species, particularly for animals that inhabit relatively homogeneous habitats and travel in groups such as schooling, pelagic fish (Dagorn et al. 2001). Despite the fact that a large number of commercially exploited fish species fall into this category (e.g. tuna, Partridge et al. 1983, herring, Nøttestad et al. 1996, mackerel, Glass et al. 2006) and that group movement is likely to influence stock size estimates (Newlands et al. 2006) for these species, only few attempts (Turchin 1989, Turchin 1997) have been made at linking aggregation and movement behavior. This is primarily due to the difficulty of simultaneously collecting movement data on multiple individuals from the same school (Dagorn et al. 2001).

In recent decades, technological progress in the field of biotelemetry (the remote monitoring of an organisms condition, activity, or function, Cooke et al. 2004) has allowed the collection of vast amounts of data on the movement of free-ranging marine animals, providing new insight into the movement ecology of a large range of species. However, the progress of methods for analysing these data has lagged behind in a lot of cases and the potential of biotelemetry for answering the key questions outlined above has yet to be fully exploited.

1.2 Fish tracking techniques: a historical overview

In the marine realm, collecting data on the movement of animals that are often highly mobile and free ranging has been notoriously difficult, particularly for non-surfacing animals such as fish. The oldest and most basic form of tracking fish movement is the external marking of individuals, a method that has been in use since at least the 1600s (McFarlane et al. 1990). The

extensive application of this method for a broad range of species started in the 1800s and increased considerably since the 1940s, when the rapid expansion of commercial fisheries after World War II required increased monitoring of exploited fish stocks (Kohler & Turner 2001). Since then, the marking of fish has provided valuable insight into the large-scale movement of a large number of fish species such as cod (Ames 2004), tuna (Eveson et al. 2009) and snapper (Patterson et al. 2001) and is a standard component of the monitoring programs for most commercial fish stocks (e.g. Hallier 2008). However, mark-recapture tagging only provides two locations from the life-history of an individual, the location where it was marked and the location of its recapture, with the latter often highly dependent on the spatial distribution of fishing effort (Sibert & Hampton 2003).

To overcome these limitations, researchers have been working on the development of electronic tags since the 1950s (Arnold & Dewar 2001). These electronic tags can be divided into two broad categories:

(1) data logging tags, which measure and record data on the animal's environment
(2) transmitter tags, which continuously transmit a signal, making the tagged animal and its location and/or presence detectable to a suitable receiver.

Data logging tags are the more recent technological development of the two, deployed on fish for the first time in the 1990s, when data-logging computers small enough to not impede the swimming behavior of fish, yet with sufficient battery power and storage capacity to record and store large amounts of data were developed (Sims 2009). The first generations of data loggers recorded pressure, providing information on the vertical movement of animals (Arnold &

Dewar 2001) and temperature, providing information on the habitat encountered by fish (Metcalfe & Arnold 1997). In the mid 1990s, light level sensors were added to tags deployed on southern bluefin (Gunn et al. 1994) and Pacific bluefin tuna (Itoh et al. 1997), allowing the estimation of geographic position from tag data using geolocation (Wilson et al. 1992) and consequently the reconstruction of the animal's movement track. Similar to traditional marker tags, however, data loggers relied on the recapture of tagged animals, making them suitable for species with high recapture probabilities i.e. commercially exploited species only. This changed in 1998 when the first pop-up satellite archival tag (PSAT) was developed (Block et al. 1998) and later fitted with a light level sensor for geolocation to study the large-scale movement of Atlantic bluefin tuna (Block et al. 2001). These PSATs are data loggers which collect and store data, detach from the animal after a predefined period and transmit the collected data via satellite. PSATs are now the standard method for studying the large-scale, open-ocean movement of non-surfacing marine animals and have provided a wealth of information on the movement ecology of a large variety of species such as turtles (Swimmer et al. 2009), sharks (Bonfil et al. 2005) and marlin (Domeier 2006). Yet, while the development of new statistical methods has considerably improved the reconstruction of animal tracks from geolocation data over the last 10 years (Nielsen et al. 2006, Pedersen et al. 2008, Jonsen et al. 2012), position estimates are still relatively coarse, particularly in coastal areas where sea surface temperature is highly variable and cannot be used to improve geolocation accuracy. Hence, signal transmitter tags are generally used for the observation of more fine-scale and coastal movement patterns.

Transmitter tags, which continuously transmit a signal, making the tagged animal and its location or presence detectable to a suitable receiver were first developed for underwater applications by the U.S. Bureau of Commercial Fisheries and the Honeywell Corporation in the 1950s. Tags emitting ultrasonic frequencies (30-300kHz) (Arnold & Dewar 2001), allowing them to be detected by a sonar or hydrophone, were deployed to track the movement of Chinook salmon in the Columbia River (Trefethen 1956). This first generation of tags was relatively large, preventing their use on smaller fish. Additionally, detections of the tag had to be recorded manually (Trefethen 1956), hence only active tracking of single tags was possible and studies using the technology focused on the small-scale movement of individual fish (Voegeli et al. 2001). From the first prototype, tags evolved rapidly and by the early 1960s a smaller tag with twice the detection range and three times the battery-life had been developed (Novotny & Esterberg 1962). In the 1970s, multichannel tags which could measure both internal and external temperature (Carey & Lawson 1973) or swimming speed (Scariotta & Nelson 1977) and transmit the data through ultrasonic codes were developed, vastly increasing the biological and behavioral information that could be collected. However, receivers were still only capable of active or “focal tracking” (Sims 2009) of single tags until the 1980s (Voegeli et al. 2001) and while providing continuous tracks with relatively high position accuracy, actively tracking highly mobile species for long periods of time is prohibitively expensive and has only been carried out for a small number of individuals from a few species (e.g. the blue shark, Carey et al. 1990, marlin, Block et al. 1992). The introduction of commercially available automated receivers in the 1980s (McKibben et al. 1985) which contained a microprocessor and memory revolutionized the use of acoustic telemetry. The microprocessor allowed the new receivers to

compare acoustic signals to a list of stored signals and thereby identify and distinguish multiple tags and the memory allowed the storage of detection records, removing the need for manual, real-time recording of detections (Voegeli et al. 2001). This allowed continuous monitoring of the presence of multiple tagged individuals at fixed locations over long time periods, such as the presence of hammerhead sharks at seamounts (Klimley et al. 1988) or tuna (Dagorn et al. 2007) or dolphinfish (Taquet et al. 2007) at fish aggregating devices . Since the development of these first automated receivers, acoustic telemetry technology has become almost ubiquitous in marine movement behavior studies (e.g. Lacroix & McCurdy 1996, Klimley & Holloway 1999, Welch et al. 2006, Dagorn et al. 2007) and the reduction in cost of acoustic receivers has meant that monitoring arrays have continuously increased in size with arrays of up to 400 receivers reported in recent studies (Welch et al. 2011). This increase in array size means that the possibilities for array configuration have become increasingly diverse (see Heupel et al. (2006) for review), giving researchers the flexibility to address a wide range of questions regarding the movement of marine fish from the fine-scale movement of reef fish (Bolden 2001) to the large-scale migration of wide-ranging apex predators (Jorgensen et al. 2010).

1.3 Automated acoustic telemetry: Array designs

The different types of automated acoustic receiver array designs can be divided into three broad categories which are not mutually exclusive and can be combined in a single array, depending on the study objectives (see Heupel et al. (2006) for full review):

(1) Single receivers placed at ecologically significant locations such as refuge areas (Meyer et al. 2000), seamounts (Klimley et al. 1988), fish aggregating devices (FADs) (Dagorn et al. 2007) or oil rigs (Lowe et al. 2009). This is the oldest automated acoustic array type (Klimley et al. 1988) and is highly suited to studying different types of aggregating behavior. It has provided significant insight into the temporal dynamics of residencies (Ohta et al. 2005) and interactions between individuals (Klimley & Holloway 1999) and species (Klimley & Butler 1988) at a given location and is the most cost and labor effective array type. While it can also be used to determine movement rates between multiple such significant locations (Lowe et al. 2009), compared to the other array design types, this generally produces the most rudimentary data in terms of recording animal movement in space and time.

(2) Regular or irregular grid arrays, which are mainly used to study the space-use of fish in well defined study areas such as reefs (Claisse et al. 2011), marine protected areas (MPAs)(Meyer et al. 2010) or coastal embayments (Heupel et al. 2004). This type of array is used to determine general movement patterns at local (meters) to regional (kilometers) scales. Detection probability depends on receiver density and is a trade-off between the size of the study area and the cost of acoustic receivers. If sufficient receivers are deployed that detection ranges overlap, continuous monitoring of fish movement is possible with a positional accuracy equivalent to the receiver range (Heupel et al. 2006). If receivers are only as far apart as the radius of the detection range, positional accuracy of 1-5m can be achieved through triangulation from simultaneous detection of a signal at three or more receivers (Andrews et al.

2011), providing complete movement tracks similar to those from active tracking. Receiver grids can be regular, random or stratified by habitat type, depending on the study objective.

(3) curtains or gates of receivers with overlapping ranges to capture the passage of animals, for example along migratory routes (Honda et al. 2010), in longitudinal coastal areas such as estuaries (Andrews et al. 2010) or in and out of MPAs (Barnett et al. 2011). This type of array is generally used to study large-scale movements (Welch et al. 2002) or in study areas too large to make gridded arrays feasible. If receiver density in a gridded array becomes too low, tags might not be detected by the array. Curtains overcome this problem by focusing receiver effort in crucial areas. While this means that tags might only be detected for a small proportion of an animal's track, detection probabilities can be close to 100% when the animal passes through the curtain (Heupel et al. 2006). If two closely spaced curtains are deployed, direction of travel can be established from subsequent detections at the two curtains (Lacroix et al. 2005).
The choice of array configuration depends both on the study objectives and the resources available and can result in widely different types of data (Heupel et al. 2006). Hence the type of data analyses that will be employed should be considered early in the design process to ensure the most efficient use of resources and successful testing of a given hypothesis.

1.4 Automated acoustic telemetry: Data analysis

The main difference in the types of data that can be collected using automated acoustic arrays is whether the temporal and spatial resolution is sufficient for the data to approximate continuous movement tracks or whether the data has to be treated as presence/absence

records at a series of fixed locations. For the former a number of descriptive movement metrics such as swimming speed, turning angle and tortuosity can be calculated (Sims 2009). More recently, a number of methods such as optimal Levy flight (Sims 2009) or state-space modeling (McClintock et al. 2011, Breed et al. 2012, Jonsen et al. 2012, Langrock et al. 2012) have been developed to determine the animal's behavioral mode such as foraging or transiting from these movement metrics in order to link behavior to spatial location.

For the presence/absence type of acoustic tracking data on the other hand, development of analytical methods has lagged behind the technological advances in the field (Heupel et al. 2006). This is due to the difficulty of dealing with data that shares the multi-dimensionality of movement tracks but is much sparser, both spatially and temporally. A common way of dealing with the multi-dimensionality of the data is to reduce the data to either the spatial or the temporal dimension. In a large number of studies, indices of residency at individual receivers or groups of receivers are computed and then linked to categorical (e.g. habitat, Afonso et al. 2009) or numeric (e.g. salinity, Collins et al. 2008) variables using standard correlation or regression approaches. A more complex analysis of residency patterns is the calculation of home ranges (Lowe et al. 2003, Heupel et al. 2004), generally from gridded array data, using methods such as kernel density estimation, Dirichlet tessellations or Delauney triangulations (Sims 2009). While these residency based methodologies can provide important insight into an animal's space-use, they ignore the temporal dimension of detection sequences and hence do not fully exploit the information held within the data. A different suite of methods on the other hand, examines temporal patterns, but treats receivers as separate entities, thus ignoring the

spatial dimension of the data. These analytical approaches include survival analysis of residence times (Klimley & Holloway 1999), time series composition to determine periodicity in detection sequences (Ohta et al. 2005) or circular statistics to determine diel rhythms in detections (Barnett et al. 2012a).

Novel quantitative approaches for the rigorous statistical analysis of data from automated acoustic telemetry arrays that include both the spatial and temporal dimensions are required in order to make the most efficient use of the wealth of data collected using this now ubiquitous technique (Heupel et al. 2006, Sims 2009, Jacoby et al. 2012). These novel methods could either be adapted from terrestrial telemetry applications (Heupel et al. 2006), from different scientific disciplines (Jacoby et al. 2012) or from methods for traditional mark-recapture analysis (Heupel & Simpfendorfer 2002), which shares many of the characteristics and problems of acoustic tracking data.

1.5 Network analysis

Network analysis is a method for quantifying and analysing the relationships between a finite set of objects (Cantwell & Forman 1993). Its concepts originate from mathematical graph theory, which can be traced back to the 18th century (Biggs et al. 1986). A network consists of nodes, which represent the objects and edges, which connect the nodes of the network and represent the relationships between them (Harary 1972). Network analysis can be used to quantify both the global properties of a network such as how well connected or clustered it is and the properties of each node such as how central to the network each node is or what effect the removal of a given node has on the network (Rhodes et al. 2006). Since the definition of

what constitutes a node and how the connection between nodes is quantified is completely open, network analysis can be applied to a large variety of systems, from a wide range of fields providing insight into networks such as the internet (Doyle et al. 2005), transportation routes (Guimera et al. 2005), human social networks (Liben-Nowell et al. 2005) or metabolic networks (Jeong et al. 2000).

In the field of animal behavior, network analysis has been applied to two different types of networks: (1) animal social networks and (2) spatial ecological networks.

Social network analysis originated in the social sciences in the 1930s (James et al. 2009) to understand patterns of human interactions. The nodes in social networks generally represent individuals and the edges between them some measure of their association. Network analysis has been applied to determine the social structure of a wide range of animal populations, both terrestrial (African elephants, Wittemeyer et al. 2005, African buffalo, Cross et al. 2004, primates, Flack et al. 2006) and marine (bottlenose dolphins, Lusseau et al. 2003, killer whales, Baird & Whitehead 2000, sharks, Mourier et al. 2011). Association strength between individuals is often defined by the "gambit of the group", i.e. the frequency with which two individuals are found together in the same group (Cairns & Schwager 1987). The definition of what constitutes a group can be explicitly social, such as grooming pairs (Flack et al. 2006), but also spatial, such as animals using the same refuge site (Godfrey et al. 2009). The flexibility of using such a spatial definition of grouping means that social network analysis has the potential to be applied to automated telemetry data to determine the link between aggregation and movement

behaviour as well as individual or species interactions at a given receiver site, which has thus far only been done descriptively (Klimley & Holloway 1999).

In spatial ecological networks on the other hand, nodes represent locations such as habitat patches (Bunn et al. 2000) or roosting sites (Fortuna et al. 2009) instead of individuals and the edges between them represent some kind of ecological flow or connection. Spatial network analysis was first applied to movement ecology by Urban & Keitt (2001) to determine connectivity of different landscapes through American mink and prothonotary warbler movement. Rather than using movement observations, however, they used dispersal probability based on simple movement rules to quantify connectivity between landscapes. A similar approach was then applied to actual movement observations for the first time to determine the properties of a network of bat roosting sites and identify priority areas for conservation using radio-telemetry data (Rhodes et al. 2006). Since then, spatial network analysis has only recently been applied to a marine species using acoustic telemetry data (Jacoby et al. 2012) and the full range of quantitative methods network analysis provides for the analysis of acoustic telemetry data has yet to be fully exploited.

1.6 Markov chain analysis

A Markov chain (Taylor & Karlin 1984) is a stochastic process, describing the transitions from one of a finite set of states to another, in which the transition probability of moving from one state to the next is only dependent on the present state, not on preceding states. While the underlying mechanisms of Markov chains are not necessarily random, they are deemed

stochastic, as transition probabilities are estimated from empirical state sequences rather than being the result of a set of deterministic rules (Johnson et al. 2004).

What constitutes a state is hereby entirely open and Markov chain analysis has been applied to such diverse phenomena as the probability of daily rainfall (Jimoh & Webster 1996), the rate of transition from preclinical to clinical state of breast cancer (Duffy et al. 1995), vegetation succession in response to climate variability (Stephenson et al. 2006) or to model transition probabilities between behavioral states in state-space models of animal movement tracks (Patterson et al. 2009, Langrock et al. 2012, Xydes et al. 2013). In animal movement analysis, Markov chain analysis has also been used to determine transition probabilities between spatial states, i.e. geographic locations or areas, from continuous animal track data (Johnson et al. 2004, Pedersen et al. 2011)

Transition probabilities can not only be estimated for states observed in the data but also for unobserved states using maximum likelihood estimation, if the adjacency matrix, i.e. the matrix defining which transitions between states are possible is defined (e.g. Deriso et al. 1991). This makes Markov chain modeling also highly suitable for elucidating transition probabilities from relatively sparse datasets. Traditional mark-recapture datasets represent such a sparse case and Markov chain models have been used to successfully determine movement probabilities between discrete spatial states from these data for a number of commercially exploited marine species such as shrimp (Grant et al. 1991), sablefish (Heifetz & Fujioka 1991) and tuna (Deriso et al. 1991, Eveson et al. 2009). Despite these successful applications, Markov chain modeling has

rarely been used to analyse animal movement patterns from automated telemetry data, even though the data is relatively similar to mark-recapture data, as it consists of repeated presence/absence records of identifiable individuals rather than actual movement tracks. The only Markov chain analysis of fish movement patterns from such data is a study of juvenile salmon migration in a river, using a radio-telemetry curtain array (Steel et al. 2001). However, since the migratory movement of juvenile salmon is unidirectional, the authors did not model movement between discrete spatial states directly. Instead, they estimated river segment specific probabilities of switching between a moving and a holding state based on travel times between curtains.

Hence, even though Markov chain analysis has been applied to mark-recapture data for decades and is increasingly being used to model movement patterns from telemetry data of complete movement tracks, the full potential of Markov chains for analysing automated acoustic telemetry data has yet to be fully realized.

1.7 Thesis objectives and structure

This thesis aims to develop novel methods for quantifying the movement behaviour of highly mobile free-ranging fish using automated acoustic tracking data and answer ecological questions of management relevance. Two automated acoustic telemetry datasets (Chapters 2 and 4) representing two common types of receiver arrays are analysed using network analysis and Markov chain modelling to quantify aggregating behaviour and space-use patterns. One of the acoustic datasets (Chapter 4) is analysed to determine the animals' local-scale sex-specific

movement behaviour, in light of the detection of sex-specific patterns in large-scale movement through pop-up satellite archival tagging (PSATs, Chapter 3).

All data chapters in this thesis have been prepared as independent, self contained manuscripts for publication. Chapter 2 has already been published in a peer-reviewed journal (Appendix 1) and chapter 3 is currently under peer-review.

The first dataset (Chapter 2) consists of acoustic tracking data from yellowfin tuna (*Thunnus albacares*) at fish aggregating devices (FADs) around the Hawai'ian island of Oahu and represents the type of array that consists of single receivers placed at ecologically significant locations. Social network analyses are applied to the data to determine the frequency and temporal dynamics of spatially and temporally explicit co-occurrences of individual tuna to elucidate the emergent structure and temporal stability of the tuna aggregations. Spatial network analyses are used to quantify movement rates between FADs and link these to the temporal dynamics of the aggregations.

The second dataset (Chapter 4) consists of acoustic tracking data from broadnose sevengill sharks (*Notorynchus cepedianus*) in a coastal area in south-eastern Tasmania and represents a curtain type acoustic receiver array. Social and spatial network analyses and a Markov chain model are applied to the data to determine local-scale sex-specific differences in space-use for this species, which were evident in the analysis of the species' large-scale movement and vertical habitat preferences from PSAT data from 5 male and 5 female broadnose sevengill sharks (Chapter 3).

Chapter 5 summarizes the findings from the three data chapters, discusses the suitability of the network and Markov approaches to acoustic telemetry data in general and different types of array designs specifically and makes suggestions for further developments of the quantitative analysis of movement behaviour from acoustic telemetry data.

Chapter 2 - Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean

2.1 Introduction

Aggregations in the distribution of individuals are an almost universal phenomenon in living organisms of all sizes, from bacteria to whales (Parrish & Edelstein-Keshet 1999). They can be considered as part of a continuum of group integration, ranging from highly territorial organisms with minimal group interaction on one end to social animal groups with strong, long-lasting bonds between individuals (Parrish et al. 2002) such as groups of primates (Flack et al. 2006) or marine mammals (e.g. Baird & Whitehead 2000) on the other. Aggregations where animals display collective coordinated movement without forming stable social bonds such as flocks of birds, insect swarms and fish schools fall somewhere between these two extremes (Parrish et al. 2002).

The behaviour of schooling fish has been the subject of many studies, both empirical (e.g. Ward et al. 2002) and theoretical (see Giardina 2008 for review). Yet, while the last few decades have seen a vast amount of data collected on the movement of free ranging animals that display some degree of collective motion (Cooke et al. 2004), the analytical approaches for quantifying collective movement from these data are relatively limited. With a few exceptions (Minta 1992), the majority of studies either determine temporal synchronicity of movement parameters such as speed or movement angle through time-series decomposition (Polansky et al. 2010; Polansky & Wittemyer 2010), ignoring spatial locations or calculate home range

overlap which uses spatial locations but ignores the temporal dimension inherent in movement data (e.g. Dillon & Kelly 2008; Schuttler et al. 2012).

Network statistical analysis has emerged as a powerful tool for improving our understanding of animal interactions, particularly in fission/fusion societies, where groups are highly dynamic and frequently split and reform (James et al. 2009). Since it relies on the temporally explicit observation of associations between individuals, to date, it has mostly been applied to determine the structure of groups of highly social species such as primates (Flack et al. 2006), insects (Fewell 2003) and marine mammals (e.g. Baird & Whitehead 2000). In these species, associations can generally be defined by socially meaningful interactions such as grooming, performing tasks together or being sighted together in social groups. The definition of what constitutes an association however, is open, which means that network analysis is highly flexible and adaptable to a number of applications, beyond the analysis of social networks. By defining an association as two individuals being present at the same spatial location at a given time, network analysis allows the quantification of synchronous movement, which includes both spatial and temporal information from animal location data, collected using a range of techniques from simple visual surveys to highly sophisticated acoustic telemetry. We used network analysis to determine patterns of co-occurrence of acoustically tagged yellowfin tuna (*Thunnus albacares*) in a network of fish aggregating devices (FADs) equipped with acoustic receivers.

Tropical tuna are amongst a number of pelagic fish species that are known to aggregate around floating objects (Fréon & Dagorn 2000; Castro et al. 2002), forming large, multi-species aggregations (Schaefer & Fuller 2005). While the biological or evolutionary advantage of the association of tuna with floating objects is not known, several hypotheses have been proposed (Fréon & Dagorn 2000; Castro et al. 2002). One of these is the meeting point hypothesis, which suggests that tuna associate with FADs to increase encounter rates with other individuals (Dagorn & Fréon 1999; Fréon & Dagorn 2000; Soria et al. 2009). If this is the case, floating objects play an important role in tuna aggregation behaviour.

The aggregation behaviour of tuna around floating objects has been exploited by tuna fishermen for decades, originally by fishing around natural floating objects such as logs and since the 1980s, by deploying both drifting and moored artificial fish aggregating devices (FADs) to enhance catch rates (Fréon & Dagorn 2000; Moreno et al. 2007). This practice has rapidly become an integral part of tropical tuna fisheries the world over and official numbers state that in 2009, 95 % of all floating objects utilized by tuna fishermen in the Eastern Pacific Ocean were man-made and 98.5 % of the total bigeye, 68 % of the total skipjack and 15 % of the total yellowfin catch were captured at FADs (IATTC 2010). Hence, understanding the dynamics of tuna aggregations at floating objects is important for determining whether this anthropogenic increase in floating object density might have a lasting impact on tuna behaviour (Soria et al. 2009).

While several studies have monitored the behaviour of individual tuna associated with floating objects (Holland et al. 1990; Cayré 1991; Marsac & Cayré 1998; Itano & Holland 2000; Girard et al. 2004; Ohta & Kakuma 2005; Schaefer & Fuller 2005; Dagorn et al. 2007), none of these studies have attempted to quantify the collective movement of tuna in FAD aggregations beyond the description of synchronous departures from and arrivals at a FAD (Klimley & Holloway 1999; Ohta & Kakuma 2005). In this study we used passive acoustic tracking to observe the presence of tropical tuna in an array of 13 FADs around the Hawai'ian island of Oahu. We analysed these data using network analysis in order to; (1) Identify the spatially and temporally explicit co-occurrences of individual tuna; (2) determine the frequency and temporal dynamics of these co-occurrences to elucidate the emergent structure and stability of the tuna aggregations. Combining the results from this novel application of network analysis with information on between-FAD movement, we attempted to identify the potential influence of artificial FADs on tuna school cohesion and mixing.

2.2 Materials and methods

2.2.1 Data collection

The Division of Aquatic Resources of the US state of Hawai'i maintains an array of 56 anchored FADs in the Hawai'ian archipelago to enhance the pelagic fishery. Thirteen of these FADs that surround the Hawai'ian island of Oahu (Fig. 2.1) were equipped with VR2 (Vemco, Halifax, Canada) automated acoustic receivers by the University of Hawai'i. Receivers were mounted directly to the FAD mooring system 18 m below the surface with the hydrophone element in a downward orientation. Acoustic receivers can detect uniquely coded VEMCO transmitter tags when within detection-range of the receivers. Range testing showed the detection range to vary between approximately 600 and 1100 m depending on local conditions. Minimum depth at the FADs was approximately 560 m. Receivers were operational throughout the deployment period, continuously collecting and storing data of the date and time of presence of tagged individuals. The data used in this study consist of 86 yellowfin (YFT) tuna captured at seven of the 13 FADs (Fig. 2.1). Tuna were captured within 500 m of FADs using surface trolling lures or baited lines with circle hooks fished to a depth of approximately 75 m. Single hooks with crimped barbs were used to minimize damage and expedite release of the fish. Immediately after capture, fish were placed in a wetted, padded cradle where the hook was gently removed and the eyes covered with a wet artificial chamois material while a saltwater hose was inserted in the mouth to provide oxygen to the gills. Tags were only placed in healthy fish with no significant bleeding from the mouth and no injury at all to the eyes or gills. We inserted tags in the peritoneal cavity using standard fish tag implantation techniques (e.g. Meyer & Holland

2000; Schaefer & Fuller 2002; Robert et al. 2012b). A scalpel was used to make a 1–2 cm long incision in the muscle of the abdominal wall 3–5 cm anterior to the anus and 2–3 cm to one side of the ventral midline. To avoid possible damage of organs by the scalpel, final entry into the abdominal cavity was made using a latex gloved finger to rupture the peritoneal lining. A coded Vemco V16 tag (69 kHz, V16-4H-R256, 5–30 s delay, rated battery life 344 days) was then inserted in the peritoneal cavity and the wound closed with two absorbable sutures. Tag weight was approximately 24 grams, which constitutes an average of 0.84 % and a maximum of 3.4 % of the total bodyweight of the tagged fish. In order to make tagged fish noticeable to fishermen and maximize reporting of recaptures, all tagged fish were also marked with an external Hallprint 11 cm plastic dart tag inserted through the pterygiophores of the second dorsal fin. All fish were measured to the nearest cm prior to release. The total elapsed time that the fish were out of water was between 1 and 2 min, with all fish released within 300 m of the FAD of capture.

Tuna were tagged in three tagging periods: 46 of the tuna were tagged from August to November 2002 and from January to May 2003 and an additional 40 fish were tagged from January to February 2005. Fish tagged in 2002/2003 ranged from 54 to 86 cm in fork length (FL) whereas fish tagged in 2005 ranged from 23 to 83 cm FL. As a previous study has shown a shift in feeding behaviour when yellowfin tuna in the Hawai'ian FAD array grow larger than approximately 50 cm FL (Graham et al. 2007), we separated our dataset along this threshold to determine the influence of size on collective movement behaviour. All fish tagged in 2002/2003 were of medium size (>50 cm FL, mean size=71.9 cm) whereas 24 of the individuals tagged in

2005 were small (<50 cm FL, mean size=36.3 cm) and 16 of medium size (>50 cm FL, mean size=71.2 cm). Tags used in 2002/2003 acoustically transmitted a unique ID code every 5-30 seconds, whereas those used in 2005 transmitted every 30-90 seconds. Tags had a battery life of 344 days, which means overlap between fish tagged in 2005 and those tagged in previous years (2002 and 2003) was not possible. The dataset of detections at the 13 acoustic receivers was therefore split in two and any subsequent analyses carried out separately for the 2002/2003 and the 2005 datasets. Where appropriate, interannual comparisons were only carried out between the 2003 dataset and the medium sized fish tagged in 2005 to remove the potentially confounding effect of fish size.

2.2.2 Animal ethics

All fishing, tagging and general animal handling procedures were in accordance with established best practices used in numerous other studies on similar sized tuna around the world (Klimley & Holloway 1999; Schaefer & Fuller 2002; Ohta & Kakuma 2005; Dagorn et al. 2007; Schaefer et al. 2007). All personnel and procedures were specifically approved by the University of Hawaii Institutional Animal Care and Use Committee (IACUC). The established best practices are designed to minimize negative impacts on the tuna and direct handling of fish was limited as much as possible. No anaesthetic was used as tuna exhibit complete immobility and insensitivity to touch or manipulation for several minutes when swiftly removed from water (Brill 2002). Furthermore, the negative effects of using anaesthetics would have been considerable, as the bodywall of tuna is involved in locomotion, meaning that the anaesthetised fish would not be able to swim. Since yellowfin tuna are negatively buoyant and obligate ram

breathers, they would sink to the bottom and suffocate (Brill 2002). Hence the animals would have to be kept in water tanks on the tagging vessel with a water flow velocity similar to the tuna's normal swimming speed until full recovery, which is not feasible. The total time a tuna spent out of the water was less than 2 minutes and no adverse impact was observed in this study or has ever been reported in any other studies, based on the observation of post tagging behaviour and long detection periods of the tags (up to 150 days in this study). Any fish determined unfit for tagging due to excessive bleeding from the mouth or injury to the eyes or gills were euthanized with a blow to the head, as recommended under IACUC procedures. The specific type of fishing employed (trolling and jigging) ensured that numbers of these unfit fish were kept to a minimum. Since aggregations at the FADs around Oahu are solely comprised of tropical tuna no other species were captured or harmed as a result of the tagging operations.

2.2.3 Association calculations

In animal networks analysis, association strength is often defined by the "gambit of the group", i.e. the frequency with which two individuals are found together in the same group (Cairns & Schwager 1987). To determine the frequency of spatio-temporal co-occurrences of tuna in FAD aggregations, we defined a group as all fish present in the receiver range of a given FAD. A pair of individuals (dyad) was therefore considered associated if their acoustic signals were detected by the same receiver within a given time interval, henceforth referred to as the *sampling period*. Despite the high temporal resolution of the acoustic data, a sampling period was hereby defined to last 24 hours, as previous tagging studies have shown tuna to exhibit periodic diel movements away from a FAD without breaking the long term association with it (Ohta &

Kakuma 2005). To test whether ignoring these short term departures from the FAD aggregations has an impact on association strength between two individuals and to determine the impact of sampling period duration on the association strength between individuals, association indices were also calculated for 1 hour sampling periods and the results compared using a randomized Mantel's matrix correlation test (Schnell et al. 1985).

To calculate the association index for each dyad, the simple ratio index (SRI), recommended by Ginsberg & Young (1992) was calculated using the SOCPROG 2.4 (Whitehead 2009) extension for MATLAB (MathWorks 2010). For two individuals a and b, the SRI is computed as follows:

Eqn. 1 $SRI=X/(X+Y_{ab}+Y_a+Y_b)$

With X = the number of sampling periods in which a and b were detected together

Y_{ab}= the number of sampling periods in which a and b were observed at different FADs

Y_a=the number of sampling periods in which only a was observed

Y_b=the number of sampling periods in which only b was observed

For the SRI to be an unbiased measure of the proportion of time two individuals spend together, the dataset has to meet the following assumptions: recorded associations are symmetric and accurate, the probability of identification is independent of whether an individual is associated or not and if one individual is detected in a given sampling period, all its associates are also detected (Whitehead 2008). Acoustic tagging data is relatively robust to

these assumptions, with the main source of possible violations stemming from acoustic signal collision. If an acoustic receiver receives the signals of two fish simultaneously, it might not record either of them, or the two colliding signals may overlap and be recorded as the signal of another tag, leading to the false detection of a fish which is not within receiver range. As the risk of signal collision increases with the number of tags present within the receiver range (e.g. Topping & Szedlmeyer 2011), tagged fish are conceivably less likely to be reliably detected when associated with other individuals. This problem is addressed and to some degree alleviated by the tag manufacturer, as tags transmit their acoustic signal at a random time, between 30 and 90 s, reducing the risk of signal collision. Moreover, the potential of signal collisions to bias the association index can be reduced by using a sampling period that is relatively large (24 hours) compared to the temporal resolution of the data (10s of seconds) and by removing any potential false detections caused by signal collision. This was accomplished by removing all single records which had no additional detections within 1 hour before or after from the raw dataset.

Another potential source of violating the aforementioned assumptions is the variable range of the receivers, which means that the spatial definition of the FAD aggregation changes, hence a tagged individual just outside the receiver range will not be detected despite being part of the aggregation. However, if this bias exists, it is probably small and approximately constant.

Using the SRI allows the computation of a symmetric half matrix of associations between all dyads, with values between 1 and 0, where 1 indicates a constant association of two individuals and 0 indicates no association. This association matrix was used for all subsequent network

analyses in SOCPROG (Whitehead 2009) and the drawing of sociograms in NetDraw (Borgatti 2002).

2.2.4 Network analysis

To visualize the tuna networks for both 2002/2003 and 2005, the datasets were plotted as sociograms, consisting of nodes and edges, where each node represents an individual and the edge between them an associative link, with the thickness of the lines representing the edges proportional to the given association index.

To test whether the network exhibited preferred associations between individuals rather than being random, we determined if there was a significant difference between real association patterns and those obtained from a large number of random permutations, which were computed as described in Whitehead (2008). As tuna were rarely detected at two different FADs within the same sampling period, the permutation of associations between rather than within sampling periods was chosen, with a null hypothesis of 'no preferred companionship between sampling periods'. This means that group membership in each sampling period was permuted with the constraint that the number of associations for each animal in each sampling period was kept constant (Whitehead 2009). The coefficient of variation (CV) of the SRI association matrix for the real and permuted datasets were then compared and the null hypothesis of random association rejected if more than 97.5% of permutations had a lower CV than the observed data ($p<0.025$). The number of permutations was increased in increments of 10000 over multiple runs until p-values stabilized at 60000 permutations.

To determine the structure of the network, the individual mean and maximum of the SRI were averaged over all individuals as well as by individual tagging cohorts (fish tagged at the same FAD on the same day). To test whether associations were higher within cohorts than overall, a randomized Mantel's matrix correlation test (Schnell et al. 1985) between the association matrix and a binary matrix of whether the individuals of each dyad were from the same (1) or different (0) cohorts was carried out.

2.2.5 Analysis of movement patterns

To compare movement patterns of tagged tuna between the two tagging periods and link them to differences in spatio-temporal co-occurrences, directed between-FAD movement rates were summed for all individuals and mapped for the two study periods. Select network metrics were then calculated for the resulting movement networks, where nodes represent the FADs and ties between them represent movement rates (see Jacoby et al. 2012). The chosen network metrics were:

1. Average degree, which indicates the average number of FADs connected to each FAD through direct fish movement.
2. Density, which represents the proportion of direct connections present out of the total number of direct connections possible.
3. Fragmentation, which is the proportion of pairs of FADs that are not connected through direct or indirect fish movement.

4. Mean strength, which is the mean number of direct movements made to or from each FAD.

2.2.6 Temporal analysis

To characterize the temporal dynamics of associations between individuals, the lagged association rates (LARs) were calculated for each dyad. This procedure determines the changes in association between two individuals after a given time lag since they were last associated. It thereby calculates the probability that two animals which are currently associated will be associated a given number of time units later (Whitehead 1995). Precision of the LAR in terms of the standard error was estimated through a jackknifing procedure in which the analysis is repeated several times, removing one sampling period for every iteration (Whitehead 2009). The LAR was then plotted against time lag using a moving average method with a window size of ten sampling periods. This window size was deemed the most suitable for the given time scales after visually comparing a range of values (1-100) (Whitehead 2009) as it removed excessive noise without sacrificing the overall shape of the curve. The LAR was then compared to the null association rate (NAR), which is the probability that two animals are associated regardless of whether or not they were associated before. The point when the LAR equals the NAR is taken as the time lag after which two individuals no longer preferentially associate with each other. To determine whether animals cease to associate for behavioural reasons or due to the fact that their tag battery has expired, they have died or permanently left the FAD array, survival analysis was carried out on the time between first and last detection of each tag using the Kaplan-Meier estimate of the cumulative distribution function (CDF) computed in MATLAB

(MathWorks 2010). The probability of still being detectable and present in the FAD array was then plotted against time lag and compared to the LAR. The assumption is hereby that a decay in the LAR which is more rapid than the associated decay in the survival of an individual in the FAD array, is indicative of actual declines in association, rather than being a result of mortality, emigration or tag failure.

To attempt to identify the underlying decay characteristics of the LAR, a number of negative exponential models, which are considered suitable for fission/fusion societies (Whitehead 2009) were fitted to the data using maximum likelihood estimation. In these exponential models, lagged association rates are built up from processes that cause either the formation or breaking of an association. The breaking or formation of an association is hereby dynamic and equally likely to occur in any time interval, which means the models can cover a wide range of possible patterns in the data (Whitehead 2009). The dynamics of the LAR are the result of one or a combination of: constant companionship, different levels of casual acquaintance or rapid disassociations (Table 2.1). Since associations are not independent of each other through time, the summed log-likelihoods from the different models cannot be used for formal likelihood ratio tests for model selection. Hence Whitehead (2009) recommends using the Quasi Akaike Information Criterion (QAIC) for selecting the best model and then judging the remaining models based on the difference in QAIC (ΔQAIC) to the one with the lowest QAIC. If the ΔQAIC is less than 2, there is substantial support for the model, if the ΔQAIC is between 4 and 7 there is considerably less support for the model, if the ΔQAIC is greater than 10 there is essentially no support for the model (Burnham & Anderson 2002).

Table 2.1 Negative exponential models of association decay over time fitted to the dataset. a_1-a_4 are model parameters, td is the time lag. Models are made up of one or a combination of decay terms describing constant companionship, casual acquaintances and rapid disassociations (see Model description) (Whitehead 2009).

Model candidates	Parameters	Model description
1	0	Constant companionship
a_1	1	Rapid disassociations and constant companionship
$\exp(-a_1*td)$	1	Casual acquaintances
$a_2*\exp(-a_1*td)$	2	Rapid disassociations and casual acquaintances
$a_2+a_3*\exp(-a_1*td)$	3	Rapid disassociations, constant companionship and casual acquaintances
$a_2+(1-a_2)*\exp(-a_1*td)$	2	Constant companionship and casual acquaintances
$a_3*\exp(-a_1*td)+a_4*\exp(-a_2*td)$	4	Rapid disassociations and two levels of casual acquaintances
$a_3*\exp(-a_1*td)+(1-a_3)*\exp(-a_2*td)$	3	Two levels of casual acquaintances

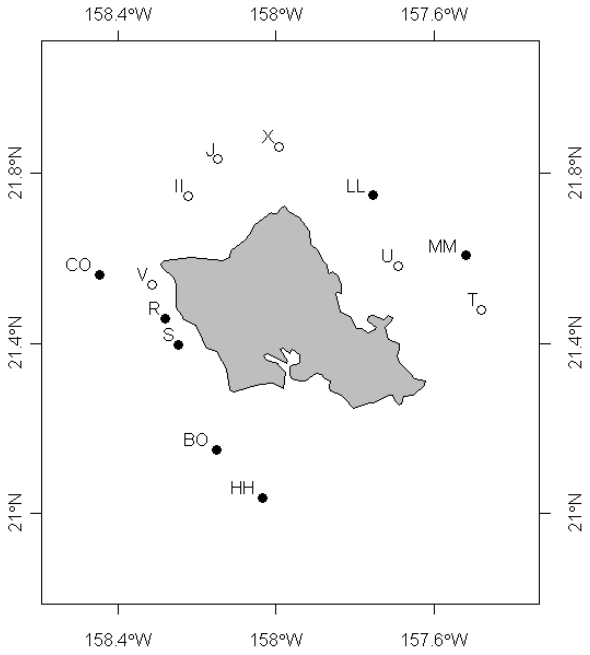


Figure 2.1 Map of the FAD array around the island of Oahu equipped with automated acoustic receivers. Filled circles indicate FADs where fish were tagged.

2.3 Results

2.3.1 Dataset overview

A total of 46 tuna were tagged in the FAD array in 2002/2003 at 5 different FADs (Table 2.2). In 2005, 40 fish were tagged at 5 different FADs, 3 of the tagging FADs were the same as during the 2002/2003 tagging (CO, HH and S). Mean tagging cohort size was similar for the 2 datasets, however, the standard deviation was greater in 2005 (Table 2.2) and the largest cohort was tagged that year (11 YFT tagged at FAD R in January 2005). The mean number of days with detections per individual was similar between 2002/2003 and 2005 whereas the total number of days with detections (i.e. total number of sampling periods) was greater in 2002/2003 due to the fact that tagging occurred over a longer time period. Mean number of fish detected per sampling period was also greater for the 2002/2003 dataset, reflecting the greater number of fish tagged.

Association matrices for hourly and daily sampling periods were strongly and significantly correlated for both the 2002/2003 (Mantel's matrix correlation = 0.964, $p<0.001$, 120 000 permutations) and the 2005 dataset (Mantel's matrix correlation = 0.983, $p<0.001$, 120 000 permutations). Subsequent analyses were therefore carried out using a daily sampling period.

2.3.2 Network structure

Associations between individuals were not random, as the coefficient of variation was significantly higher than in the randomized dataset for fish tagged in 2002/2003 (CV=3.69, random CV=3.68, $p<0.025$), and small (CV=3.26, random CV =3.17, $p<0.025$) and medium sized fish (CV=1.58, random CV=1.24, $p<0.025$) tagged in 2005. This indicates that fish associated preferentially with particular individuals over several sampling periods in all cases.

Mean association was highest for medium sized fish in 2005 (>50 cm FL), whereas small fish (<50 cm FL) tagged in the same year had a much lower mean association index. Fish tagged in 2003 (>50 cm FL) had the lowest mean association due to the tagging being carried out over a much longer time period, leading to a large proportion of zero associations (Table 2.3). When comparing the means of non-zero elements, however, fish tagged in 2003 had the highest mean association (SRI=0.321), followed by medium sized fish tagged in 2005 (SRI=0.273), while small fish tagged in 2005 had the lowest mean association (SRI=0.221).

Individuals had significantly stronger associations ($p>0.975$) with fish they were tagged with (Mantel's test t=16.39 in 2002/2003 and t=12.26 in 2005) than with other fish and mean associations within a cohort were similar across years and size classes and consistently larger than the population mean (Table 2.3). In both years fish that stayed at the FAD of tagging for a relatively long period of time (>1 week) and did not visit any other FADs had the highest mean associations.

2.3.3 Movement patterns

The 2002/2003 data indicates that individuals were much less likely to associate with individuals tagged at other FADs than in 2005 (Fig. 2.2), when the majority of fish formed associations with fish tagged at other FADs. This is due to the different probabilities to encounter fish tagged at other FADs between the two years, as more individuals moved to FADs other than their FAD of tagging in 2005 (58 % of all small and 44 % of all medium sized fish) than in 2002/2003 (17 % of all tagged fish). Yet, even though less individuals moved to different FADs, more FADs were visited by tagged fish in 2002/2003 than in 2005 (Fig. 2.3) leading to the greater mean degree and density and lower fragmentation of the movement network in 2002/2003 (Table 2.4). Between-FAD movement rates, however, were greater in 2005 than in 2002/2003 (Fig. 2.3) resulting in a greater mean strength of the movement network (Table 2.4). The large standard deviation of mean strength in 2005 was caused by the large number of movements (21) between adjacent FADs R and S. The greater between-FAD movement in 2005 also meant that detections were spread more evenly across receivers (Fig. 2.3) whereas in 2002/2003 almost half of all detections occurred at a single FAD, which had no connection to any other FADs through direct tuna movement (FAD HH).

As a result of the lower between-FAD movement rate in 2002/2003, there was an overall significant ($p<0.05$) relationship between mean number of associates and number of fish tagged per FAD (linear model, $R^2=0.93$, $p=0.007$) that year and fish tagged at FAD CO had the highest mean number of associates (Table 2.5), due to the fact that it was the FAD with the largest number of fish tagged. In 2005 on the other hand, fish tagged at FAD R had the overall

highest mean number of associates despite the fact that the largest number of fish was tagged at FAD S (Table 2.3) and there was no significant relationship between mean number of associates and number of fish tagged (linear model, R^2=0.72, p=0.07). Instead, the fish with the largest number of associates in 2005 was an individual that performed multiple between-FAD movements, visiting a total of 5 of the 13 FADs.

2.3.4 Temporal dynamics

Decay of association between dyads differed considerably between the 2002/2003 and the 2005 dataset. In 2002/2003, the probability to remain associated initially decreased slowly over a time lag of approximately 20 days and only then started to decline steeply (Fig. 2.4a). The LAR crosses the NAR at a lag of approximately 60 days, suggesting that after this lag, association between individuals was random, irrespective of whether or not the dyad was associated previously. In 2005, the LAR steeply declines from the first day and reaches the level of the NAR after a time lag of approximately 20 days (Fig. 2.4b), indicating a much faster decay of associations. There was a slight difference in association decay between small and medium sized fish in 2005, with associations decaying less steeply for medium sized fish and some re-associations occurring after 20 and 30 days. Yet, the point at which the LAR first reaches the NAR was similar for small and medium sized fish at a lag of around 20 days (Fig. 2.5). The probability of survival within the FAD array is relatively similar for the different datasets with a slightly steeper decline in the 2002/2003 data (Fig. 2.5). In the 2002/2003 dataset the LAR is generally above the survival probability, suggesting that decay in association calculated from the acoustic tracking data might be a result of fish leaving the FAD array and that actual decay

in association might be slower. In 2005 on the other hand the LAR lies below the survival probability for both size classes, indicating that emigration or removal from the FAD array is not the cause of the steep decay in association.

The differences between the 2002/2003 and 2005 data are also evident in the negative exponential models that best fit the two datasets. For 2002/2003, the model of rapid disassociations, constant companionship and casual acquaintances (see Table 2.6 for model parameter values) had the lowest QAIC. For 2005 on the other hand, the model that best fit the data was that of two levels of casual acquaintances (see Table 2.6 for model parameter values), however, there was also substantial support for the model of rapid disassociations and two levels of casual acquaintance (see Table 2.6 for model parameter values). These two model candidates were the best fit for the 2005 data when analysing the two size classes separately as well. Hence, interannual differences in association decay were real and not a result of differences in fish size. The lack of constant companionship identified in the models in 2005 is evident in the maximum total amount of time a dyad spent together in the two years. While the maximum of time two fish spent together was approximately 52 days in the 2002/2003 data, it was only approximately 10 days for medium sized fish and 18 days for small fish in the 2005 data. The mean of the maximum time an individual spent with any other tagged fish was twice as high in the 2002/2003 dataset (10 days, standard deviation=15 days) as in 2005 (5 days, standard deviation=3 days for medium sized fish, 4 days, standard deviation=5 days for small fish).

Table 2.2 Dataset overview. For mean values, standard deviation is given in brackets.

Tagging period	Tagging FADs	Number of fish	No of cohorts	Mean number of fish per cohort	Mean number of days with detections per fish	Number of sampling periods (days)	Mean number of identifications per sampling period
27/08/2002-27/05/2003	CO, HH, LL, MM, S	46 medium sized YFT (length>50 cm)	20	2.7 (1.9)	16.4 (22.4)	222	3.72 (2.30)
06/01/2005-17/02/2005	BO, CO, HH, R,S	24 small YFT (length<50 cm) 16 medium sized YFT (length>50 cm)	12	3.3 (3.1)	15.6 (13.6)	173	3.34 (3.65)

Table 2.3 Mean SRI for each individual averaged over the dataset as a whole and within tagging cohorts for small and medium sized fish. Standard deviation is given in brackets.

	Mean Association		
	2002/2003 medium	2005 small	2005 medium
Within cohorts	0.26 (0.24)	0.30 (0.30)	0.36 (0.24)
Overall	0.04 (0.04)	0.06 (0.07)	0.13 (0.08)

Table 2.4 Network metrics calculated for the tuna movement networks in 2002/2003 and 2005.

Movement network metric	2002/2003	2005
Average degree	2.769	2.154
Density	0.231	0.179
Fragmentation	0.295	0.641
Mean strength	6.31 (4.96)	9.08 (10.54)

Table 2.5 Mean number of associates per individual by tagging FAD and number of fish tagged per FAD. Standard deviation is given in brackets.

FAD	Mean number of associates 2002/2003	Number of fish tagged 2002/2003	Mean number of associates 2005	Number of fish tagged 2005
BO	-	-	4.0 (4.2)	2
CO	7.3 (3.9)	19	5.0 (1.7)	3
HH	4.7 (1.9)	9	8.6 (3.2)	8
LL	1 (-)	1	-	-
MM	0 (-)	1	-	-
R	-	-	14.8 (6.8)	11
S	5.3 (3.9)	16	11.7 (4.4)	16
Overall	5.8 (3.8)	46	11.0 (5.7)	40

Table 2.6 Negative exponential models and model parameter values of association decay over time which best fit the 2002/2003 and 2005 datasets. Two models and sets of parameter values are given for the 2005 data, as there was substantial support (ΔQAIC <2) for a second model (See Table 2.1 for descriptions of models).

Year	Model	a_1	a_2	a_3	a_4	ΔQAIC
2002/2003	$a_2+a_3*\exp(-a_1*td)$	0.021	-0.046	0.998	-	-
2005	$a_3*\exp(-a_1*td)+(1-a_3)*\exp(-a_2*td)$	0.195	0.047	0.959	-	-
2005	$a_3*\exp(-a_1*td)+a_4*\exp(-a_2*td)$	0.192	0.045	0.953	0.037	1.6

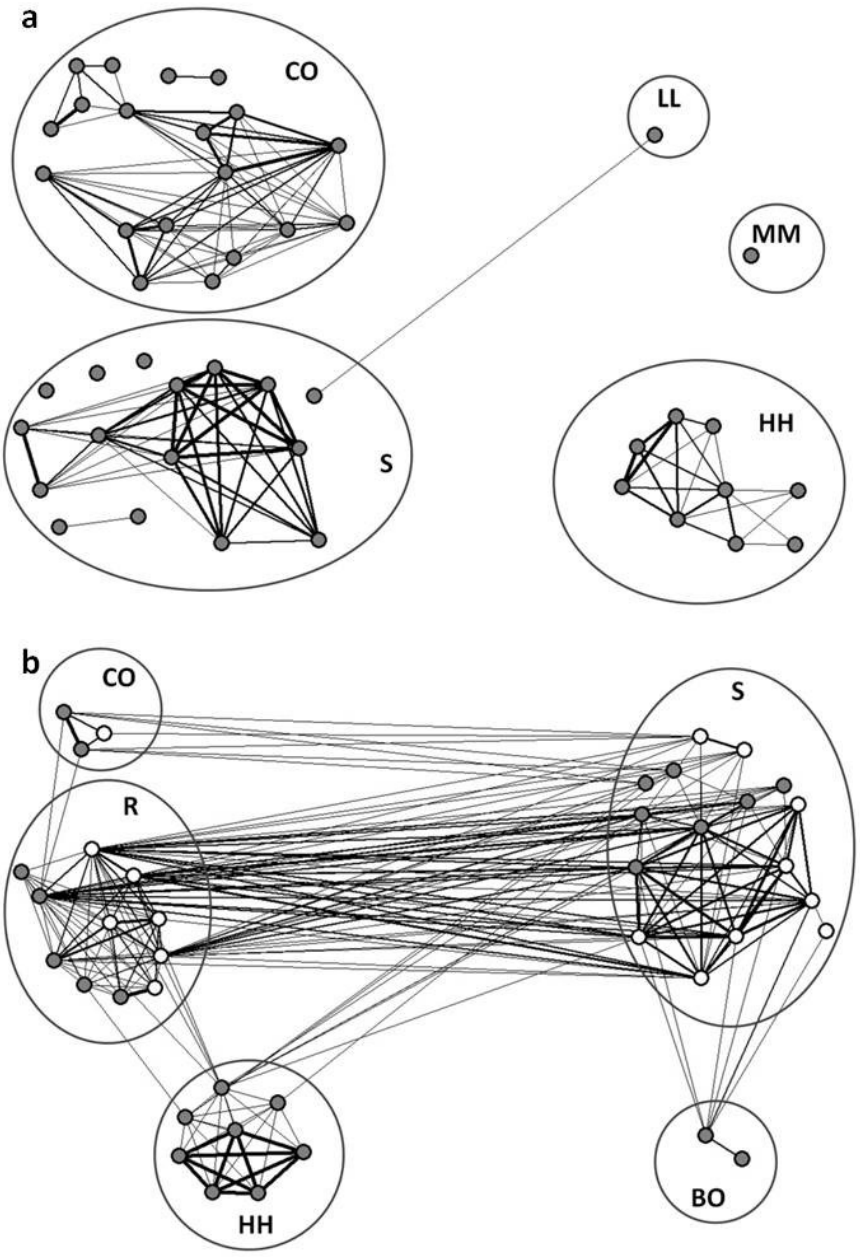


Figure 2.2 Sociogram of **a)** associations between tuna tagged in 2002/2003 and **b)** associations between tuna tagged in 2005. Ellipses indicate tagging FADs (refer to Fig. 2.1). Nodes represent individual tuna, lines represent edges between them. Line thickness is proportional to association strength calculated using the SRI. Grey nodes represent medium sized fish (>50 cm fork length), white nodes represent small fish (<50 cm fork length).

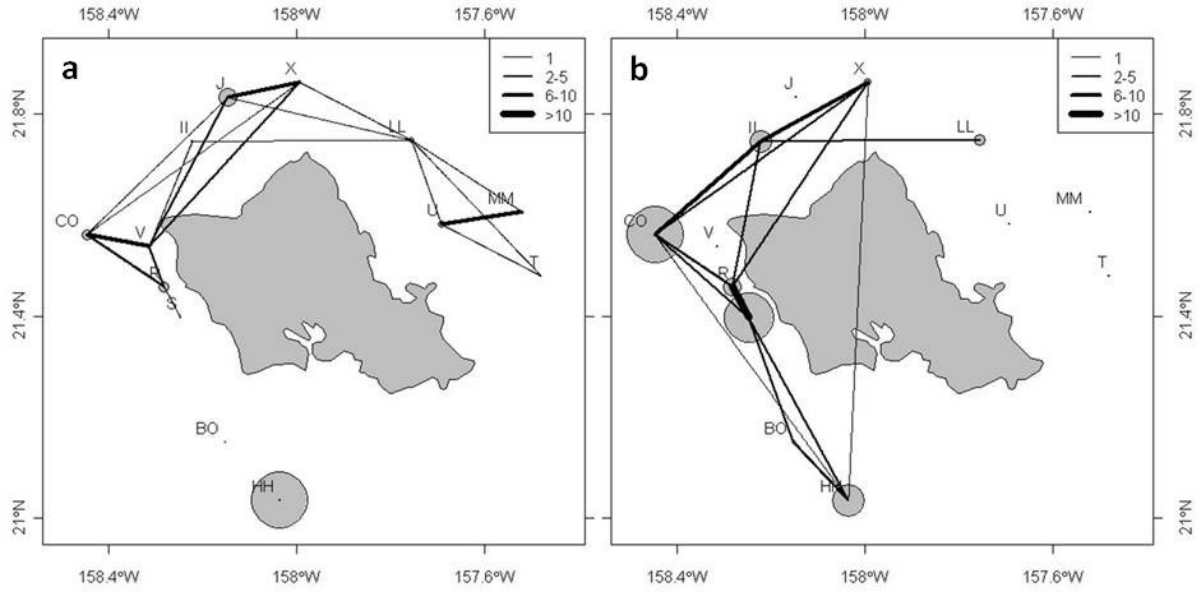


Figure 2.3 Map of the tuna movement network in the FAD array with lines showing between-FAD transitions of tagged tuna for **a)** 2002/2003 and **b)** 2005. Line thickness indicates number of times transitions were made. Size of the circles indicates percentage of total detections recorded at each FAD. In 2003 the largest percentage of detections (49 %) was recorded at FAD HH, in 2005 the largest percentage of detections (28 %) was recorded at FAD CO.

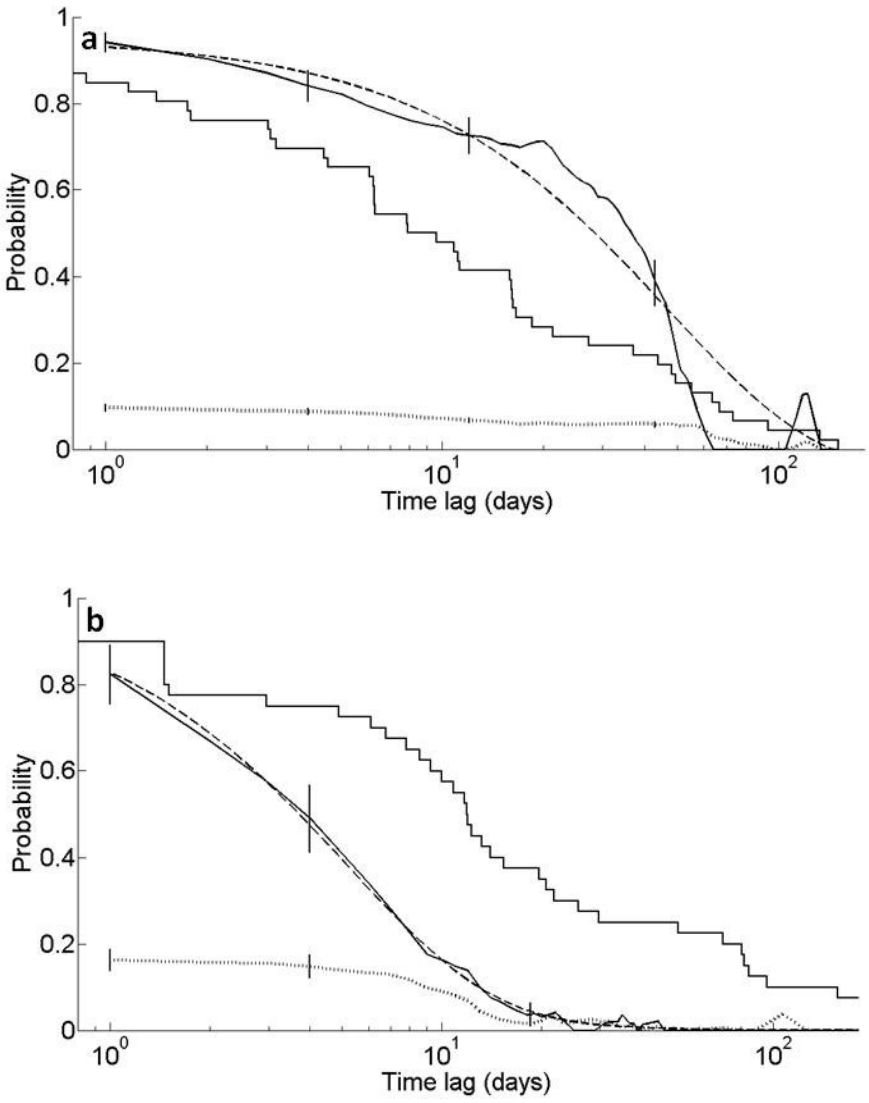


Figure 2.4 Plot of lagged association rate (LAR) (black line), null association rate (NAR) (dotted line), fitted model of exponential decay in association (dashed line) and survival probability (step function) for **a)** 2002/2003 dataset and **b)** 2005 dataset. Vertical lines extending from the LAR curve indicate precision estimates (±1 standard error) obtained from jackknifing. LAR and NAR are plotted using a moving average window of ten sampling periods. At the time lag where LAR and NAR cross, there is no preferred association between two individuals based on the fact that they were associated previously. Survival probabilities are calculated using the time from first to last detection of each individual.

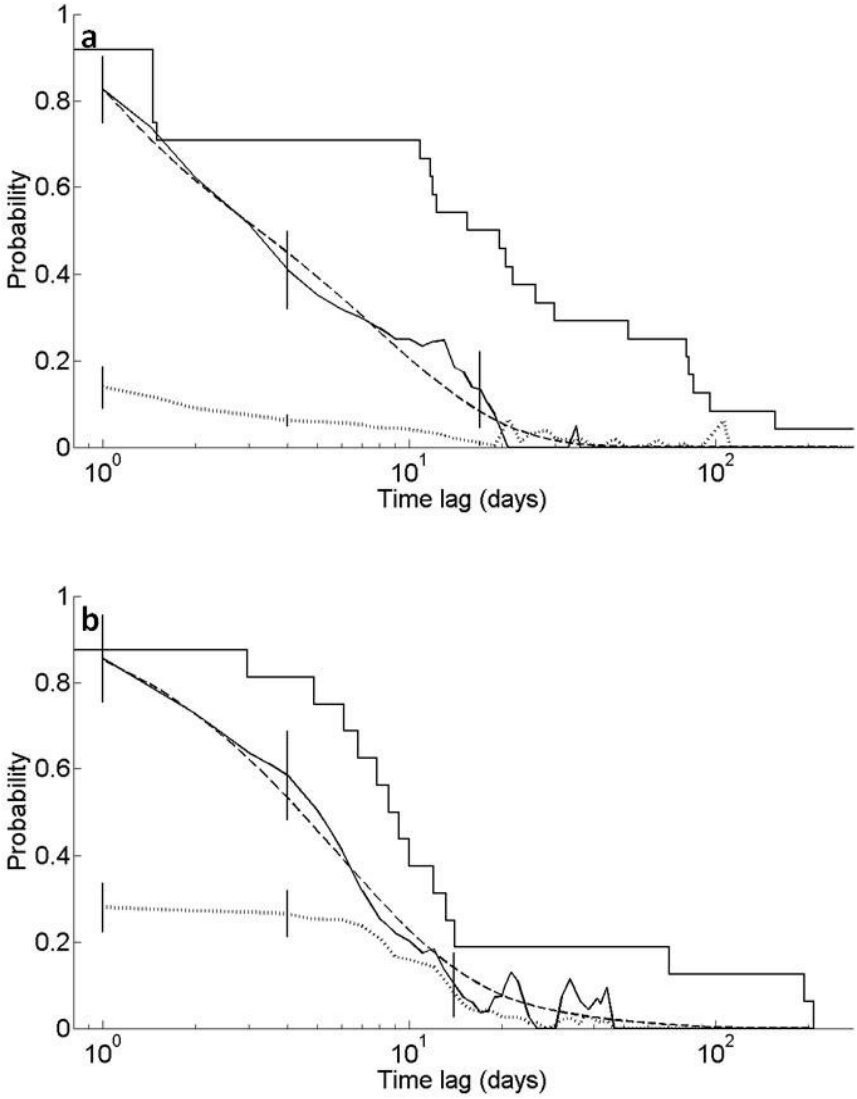


Figure 2.5 Plot of lagged association rate (LAR) (black line), null association rate (NAR) (dotted line), fitted model of exponential decay in association (dashed line) and survival probability (step function) for **a)** small fish and **b)** medium sized fish tagged in 2005. Vertical lines extending from the LAR curve indicate precision estimates (±1 standard error) obtained from jackknifing. LAR and NAR are plotted using a moving average window of ten sampling periods. At the time lag where LAR and NAR cross, there is no preferred association between two individuals based on the fact that they were associated previously. Survival probabilities are calculated using the time from first to last detection of each individual.

2.4 Discussion

Observing and elucidating patterns in co-occurrence of individuals and species in space and time is critical in deepening our understanding of a great many ecological phenomena. As well as the group-behaviour and individual movement dynamics considered here, other basic processes such as reproduction, predation and competition ultimately depend on how often individuals encounter each other. Obtaining and modelling the dynamics of these encounters is therefore of considerable importance in beginning to understand how individual encounters scale into population level processes. Many studies have examined patterns of co-occurrence or synchronous space-use of animals for a variety of species such as lions (*Panthera leo*) (Polansky et al. 2010), African forest elephants (*Loxodonta cyclotis*) (Schuttler et al. 2012) or raccoons (*Procyon lotor*) (Robert et al 2012a). Often, movement patterns are characterized by repeated presence/absence sampling at fixed points using methods such as visual surveys, camera traps or automated telemetry. Typically, estimates of home range overlap are used to determine co-occurrence of individuals from these data. However, these kinds of metrics are inherently static and ignore the temporal dimension of movement (e.g. Dillon & Kelly 2008, Schuttler et al. 2012). And while home range overlap is related to contact frequency for some species such as raccoons (Robert et al 2012a) for others such as white-tailed deer (*Odocoileus virginianus*) it is not (Schauber et al. 2007). Therefore, to progress our understanding of co-occurrence of multiple individuals, methods incorporating both spatial and temporal dimensions are required. In this study we have demonstrated how network analysis can be employed as such an approach, even in a relatively sparse, open case: the movement of free-

ranging oceanic fishes. Despite the challenges of large spatial scales and widely dispersed and sparse data collection points (the FADs) this study has shown that useful insights about the likelihood of co-occurrence may be obtained by employing the network analysis methods demonstrated here.

For tuna, a multitude of studies have employed acoustic tagging to determine their behaviour and movement around FADs, in order to elucidate any impact this now ubiquitous fishing practice might have on fish populations (Holland et al. 1990; Cayré 1991; Marsac & Cayré 1998; Klimley & Holloway 1999; Itano & Holland 2000; Girard et al. 2004; Ohta & Kakuma 2005; Schaefer & Fuller 2005; Dagorn et al. 2007; Robert et al 2012b). Prior to our study, analyses of spatio-temporal co-occurrences between individuals have been largely limited to describing events when two or more fish arrived at or left a FAD together (Klimley & Holloway 1999; Ohta & Kakuma 2005; Dagorn et al. 2007). We found that performing network analysis on the spatio-temporal co-occurrences of tuna allowed us to use the entire acoustic tracking dataset and gave us quantitative information on the frequency and temporal dynamics of these co-occurrences to elucidate the emergent structure and stability of the tuna aggregations.

The frequency and temporal dynamics of spatio-temporal associations in the yellowfin tuna aggregations in the array of FADs around Oahu showed considerable variability between the two years. Mean of non-zero associations was higher in 2002/2003 than fish tagged in 2005, while the mean number of associates was higher in 2005 and less clearly linked to the number of fish tagged at the same FAD than in 2003. This was true for both size classes tagged in 2005

and strength of spatio-temporal associations did not appear to be strongly influenced by size. This is contrary to the oft-observed pattern of strong attraction of juveniles of marine fishes to conspecifics that tends to wane as animals grow larger (Pavlov & Kasumyan 2000).

Differences between the two sampling years are most likely due to a larger percentage of fish exhibiting between-FAD movement in 2005, increasing the probability to encounter fish tagged at other FADs. Dagorn et al. (2007) who analysed the 2002/2003 dataset, found that very few fish visited FADs other than the FAD of tagging, suggesting that at the density of the given array, FADs may not modify the residence pattern of the tuna at a larger scale. Our comparison of the 2002/2003 and the 2005 datasets show that this pattern is not consistent across years. Girard et al. (2004) hypothesised that differences in between-FAD movement rates across studies might be due to fish going through an exploration stage when arriving at a FAD array, during which they move between FADs until they have found one with suitable conditions, followed by a stage of continuous association with the selected FAD. Sampling a larger proportion of fish in either of these stages during tagging will lead to considerably different estimates of between-FAD movement rates. It is also possible that differences in local conditions at the FADs across years caused differences in movement rates. Although Ohta & Kakuma (2005) found no influence of abiotic conditions on associations of tuna with FADs, they did suggest that biotic factors such as density of prey or conspecifics or presence of predators might cause tuna to leave a FAD.

In general, membership of individuals in aggregations of animals only persist as long as membership benefits, such as protection from predators outweigh memebership costs, mainly increased competition for food (Ritz et al. 2011). Hence, strength of associtions between two individuals within an aggregation is density as well as resource dependent and variability in either between years might cause differences in movement rates and resulting association strength.

While we cannot test either of these hypotheses, our analysis of the 2005 data does show that the FADs in the western part of the array (FADs R,S and V) are at a sufficient density for fish to perform repeated movements between them, and the fact that the majority of fish were tagged at the two adjacent FADs R and S in 2005 might have resulted in the high between-FAD movement rates that year. These high movement rates might be the cause of an increased mean number of associates as well as a decrease in mean association strength. Moreover, the temporal analyses of the FAD aggregations showed that associations decayed much faster between fish tagged in 2005 than between those tagged in 2002/2003, regardless of fish size. While associations in FAD aggregations did not persist for more than 20 days in 2005, they lasted for up to 60 days in 2002/2003 despite the fact that survival probabilities decayed at similar rates between years. Hence, the difference in association decay is potentially even greater, as the decline in survival probability might have caused the decay in association rate in 2002/2003, whereas this did not play a role in 2005.

Klimley & Holloway (1999) found evidence of long term companionship between yellowfin tuna in the FAD array around Oahu, based on the fact that some tagged individuals returned at the same time to the FAD of tagging, up to 5 months after their departure. In mark-recapture studies of unassociated schools of skipjack tuna, Bayliff (1988) estimated school integrity to last up to 3 to 5 months, whereas Hilborn (1991) calculated that up to 63 % of skipjack leave a school each day to join a different school.

Data from other free ranging fish species are also equivocal with no or low school fidelity detected in the yellow perch (*Perca flavescens*) (Helfman 1984) as well as the banded killifish (*Fundulus diaphanous*) (Hoare et al. 2000) and strong school fidelity detected in the three-spine stickleback (*Gasterosteus aculeatus*) (Ward et al. 2002). Intraspecific variations in estimated school fidelity are potentially due to non-uniform association patterns within aggregations (Hilborn, 1991), as more stable subunits often form in animal groups, based on common phenotype (Krause et al. 2002) or kinship (Ritz et al. 2011). It is possible that, by chance, some members of such cohesive subunits were tagged in 2002/2003 and therefore identified as constant companions, whereas this was not the case in 2005, resulting in the differences in association decay. However, it is also possible that the differences in between-FAD movement rates caused the differences in school integrity. This would mean that the FAD array at Oahu is at a sufficient density to facilitate between-FAD movement, leading to greater mixing between schools and lower school cohesion. Since the evolutionary or ecological advantage of the aggregating behaviour in tuna is still unknown, the impact of the decreased cohesion of FAD aggregations cannot be determined. However, an increased exchange of individuals between

schools has been shown to cause increased disease transmission and disrupt natural behavioural processes but also facilitate the transfer of information and social learning in other species (see Croft et al. 2003 for review).

The distance between two adjacent FADs in the Hawai'ian FAD array ranges from 7.3 to 31.1 km (Dagorn et al. 2007). These between-FAD distances are similar to some estimates of distance between adjacent FADs in other FAD arrays in the tropical Pacific, where Desurmont & Chapman (2000) reported distances ranging between 6 and 32 km. The main source of potential bias inherent in acoustic tracking data is the variability in receiver range due to variability in environmental conditions. One of the assumptions of using group membership to define associations is that if one individual is detected, all its tagged associates are also detected (Whitehead 2008). Hence, if a tagged individual is outside the receiver range but part of the aggregation, the assumption is not met. However, Cillaurren (1994) found from catch data, that the majority of tuna are caught within 500 m of a FAD (see also Moreno et al. 2007), which is well within the expected minimum receiver range of 600 m determined through range testing (Dagorn et al. 2007). Additionally, Ohta & Kakuma (2005) found that when associated with a FAD, tuna spent the majority of time within the detection range of their acoustic receivers, which had a maximum radius of 680 m.

The conceptual model encapsulated by the idea of the 'gambit of the group', which is commonly used in animal network analysis, was well suited to quantifying co-occurrences of pairs of individuals from acoustic tracking data, yet acoustic tracking technology is rarely used to study aggregation behaviour (Ritz et al. 2011). Additionally we could find relatively few

examples of the application of network analysis to quantify the co-occurrence of individuals in a non-social context. One of the exceptions to this is the study by Godfrey et al. (2009) who also used network analysis of data on presence of tagged individuals at fixed spatial locations to quantify co-occurrences of individuals as a way of identifying patterns of parasite transmission in the gidgee skink *Egernia stokesii*. They carried out a mark recapture study, which often have low sampling frequency due to the large cost and effort involved in repeated sampling and may therefore not record all connections between individuals (Godfrey et al 2009). Automated telemetry on the other hand provides near continuous monitoring of presence/absence of tagged individuals, which provides greater confidence that all co-occurrences within the area being monitored are recorded.

Given the widespread use of acoustic telemetry in marine systems and the use of radiotelemetry to identify individuals in terrestrial systems we conclude that the methodology illustrated here should have a wide application. The main limitation of the automated telemetry data used in this study was the coarseness of the grouping that can be inferred. In this case, each FAD aggregation was potentially comprised of multiple schools, which in turn were probably comprised of stable subunits. Therefore, determining the influence of FADs at high densities on the cohesion of schools requires data at even higher spatial resolution. Such data may well be collected in the future; recent advances in inter-animal acoustic telemetry (Holland et al. 2009, Guttridge et al. 2010) allow the collection of the required data in the marine realm, as novel acoustic tags are able to record when another tagged animal is within a specified radius and transmit this information to a receiver when it comes within range. Similar

technologies are already available for terrestrial applications (e.g. Robert et al 2012a) and have been used to determine individual contact rates within and between species (Boehm et al. 2009). Applying network theory to these new types of data will enable the analysis of collective motion at a much higher resolution and thereby give new insight into not only the impact of FADs on the schooling behaviour of tropical tuna but also into other questions related to the co-occurrence of individuals and species in space and time across a broad range of systems. If the spatial resolution is improved to the point where it becomes meaningful in a social context, it will furthermore allow the inclusion of sociality into the analysis of collective motion, which could be an important factor in determining how animal populations move, split up and reform (Bode et al. 2011).

Chapter 3 - Intraspecific differences in movement, dive behavior and vertical habitat preferences of a key marine apex predator

3.1 Introduction

The patterns of large-scale movements of animals tend to be driven by the integration of a number of life-history requirements such as foraging, reproduction and dispersal (Kuhn et al. 2009). Understanding these patterns is essential to understanding the impacts of anthropogenic pressures on the animals, as well as the ecosystems they frequent (Dingle 1996). This is particularly true for higher order predators, which exert considerable influence on ecosystem structure through the top-down regulation of prey species (Stevens et al. 2000).

The global decline in marine apex predator abundance and the potential ecosystem-wide ramifications are a growing concern (Baum et al. 2003, Myers & Worm 2003, Heithaus et al. 2008, Estes et al. 2011). This is particularly true for sharks, which are often slow growing, late maturing and have low fecundity, making them highly vulnerable to overexploitation (Compagno 1990). Migratory behavior is a common trait in many shark species (Speed et al. 2010) and movements can range from short seasonal (Bruce et al. 2006) to transoceanic migrations (Bonfil et al. 2005). Understanding the complexities of this behavior is essential for the development of successful conservation and management measures (Speed et al. 2010).

The broadnose sevengill shark (*Notorynchus cepedianus*) is a large (up to 3m) demersal shark of the order *Hexanchiformes* (Barnett et al. 2012b). It is one of the most important apex

predators in temperate coastal areas around the world (Last & Stevens 2009), due to the high diversity of its diet, which includes marine mammals, chondrichthyans and teleosts (Cortés 1999, Barnett et al. 2010a). While not a target species, it is often caught as by-catch in commercial shark fisheries (Compagno 1984) and targeted by recreational fishermen (Lucifora et al. 2005). Although the global fisheries status of the sevengill shark is not well known (Barnett et al. 2012b), in the Southern Australian shark fishery it is considered to be highly vulnerable to gillnetting gear and at high risk in terms of abundance and catch susceptibility (Walker et al. 2007). The current fishing mortality rate is estimated to be higher than the maximum sustainable fishing mortality (Zhou et al. 2007).

Despite its importance as an apex predator in coastal marine systems, until recently little was known about the species' ecology beyond dietary information (Ebert 2002, Braccini 2008, Barnett et al. 2010a) and it is therefore listed as data deficient on the IUCN Red List (Fowler et al. 2005). However, a number of recent studies carried out in Patagonia (Lucifora et al. 2005), the west coast of the USA (Williams et al. 2011) and Tasmania (Barnett et al. 2010c) have shed light on the population structure, and acoustic tracking studies in Tasmania (Barnett et al. 2010b, Barnett et al. 2011) and Washington State (Williams et al. 2012) have determined the fine-scale movement behavior and seasonal habitat use patterns of these animals. All of these studies showed a marked increase in abundance in nearshore areas in spring and summer, followed by a near absence in winter and individuals have been shown to display strong site fidelity in their return to certain coastal sites after winter. In Patagonia (Lucifora et al. 2005) and California (Ebert 1989), seasonal movement into nearshore areas has been attributed to

pupping activity, whereas prey abundance was considered the main factor driving the seasonal use of coastal areas in Washington State (Williams et al. 2011) and Tasmania (Barnett et al. 2010c). Upon leaving the coastal areas in autumn, sexual segregation was evident from the migratory behavior of the sevengill sharks in Tasmania. Males moved distances of up to 1000 km northward into warmer waters off the east coast (Barnett et al. 2011) or northwest to the central south coast of mainland Australia (unpublished data), whereas some females stayed in coastal areas and others left for an unknown destination, possibly offshore (Abrantes & Barnett 2011). Sexual segregation is common in many shark species (Wearmouth & Sims 2008, Speed et al. 2010) and sex biased migration has been shown for other shark species such as the white shark *Carcharodon carcharias* (Pardini et al. 2001). Sex specific differences in migratory behavior may have significant ramifications for conservation and management, if males and females are exposed to differential degrees of fishing pressure (Mucientes et al. 2009).

Pop-up satellite archival tags (PSATs), which transmit data on depth and temperature preferences of the tagged animal via a satellite link, have been successfully deployed on a number of different shark species to determine their dive behavior, habitat preferences (Hammerschlag et al. 2011) and determine the characteristics of offshore foraging areas (Nasby-Lucas et al. 2009). In this study, we analysed unpublished data on depth and temperature preferences from PSATs deployed on five male broadnose sevengill sharks by Barnett et al. (2011). We furthermore deployed PSATs on five females in their nearshore Tasmanian summer habitat just before they were due to start their annual winter migration

(Barnett et al. 2010c) to investigate a) sex specific differences in large-scale movement and b) vertical habitat preferences and movement during the sharks' winter migration.

3.2 Methods

3.2.1 Tagging of sharks

Ten pop-up satellite archival tags (MK10 PSAT, Wildlife Computers, Redmond, WA, USA) were deployed on five male and five female broadnose sevengill sharks from 2008 to 2011 (Table 3.1). These tags measure external temperature, depth and light level at user-defined time intervals, detach from the animal after a pre-programmed deployment period and transmit the collected data to the Argos satellite system. Since satellite bandwidth is limited, depth and temperature data are summarized for a specified summary period as histograms of time spent at a set of depth and temperature bins and as temperature-at-depth profiles. Since tags were deployed over four years, data returns from initial tag releases informed the programming of subsequent tags to optimize sampling efficiency, resulting in different tag setups between years (Table 3.2).

All tags were deployed in the Derwent Estuary/Norfolk Bay, a system of coastal embayments on the south east coast of Tasmania (Figs. 3.1a & b). Tagging was carried out at the beginning of the Austral winter (May/June), as seasonal longline sampling indicated migratory movement out of the coastal areas around this time (Barnett & Semmens 2012). Sharks were caught on bottom-set, baited longlines, lifted onto the tagging vessel and turned on their back. When on their back, broadnose sevengill sharks enter tonic immobility which means that the sharks could be handled without the need for restraining. Aboard the tagging vessel, the hook was

carefully removed from the shark's mouth, their eyes covered with a wet cloth to avoid injury, their sex identified and total length measured.

Tags were attached to the shark by implanting a stainless steel anchor, which was attached to the tag via a 100 mm long, nylon coated, multi-strand, stainless steel wire trace (2 mm diameter) into the dorsal musculature. A second anchor with a stainless steel wire loop attached to it, which was placed around the body of the tag, was implanted approximately 100 mm behind the first anchor to prevent excessive sideways movement of the PSAT. Aseptic techniques were used during anchor implantation and the entire procedure lasted approximately 3-5 minutes. Running seawater was continuously pumped over the gills of the shark throughout the procedure. Prior to release, a povidone-iodine antiseptic was applied to the wounds to aid healing. All methods used were approved by the University of Tasmania Animal Ethics Committee (Approval No A0011590).

3.2.2 Data analysis

Records from the first 24 hours of archival records were removed from the dataset to remove any abnormal behavior associated with tagging stress. Records following tag detachment were also removed from the dataset.

To study broad-scale movements of sevengill sharks, for each tagged individual we calculated the most probable track from the raw geolocation data using Kalman Filter analysis (kftrack package in R, Sibert et al. 2003). For the larger movements observed in this data set, this

approach is likely to be reliable. However, the typical scale of errors from light-based geolocation is too large to provide reliable track estimates for fine scale coastal movements (see Fig. 1c). The application of more sophisticated methods which improve position estimates by accounting for sea surface temperature (SST) measurements from the tags (Nielsen et al. 2006) was not possible due to the fact that the sharks spent a large amount of time in coastal areas where SSTs are highly variable. We therefore estimated minimum dispersal from the tagging location instead, by mapping the first Argos satellite transmission locations from detached PSATs with a location class of 2 or 3 (location error < 500m, CLS 2011) as the tag pop-off locations. To estimate timing of departure from the coastal tagging location, SSTs recorded by the tags (defined as any temperature values recorded at depths <5 m) were compared to monthly average SSTs at the entrance to the Derwent estuary (Derwent Estuary Program).

To examine variations in preferred swimming depth over the course of a shark's track, weighted mean depths for each data summary period were estimated from transmitted time at depth histograms as the sum of the product of the bin frequency and corresponding bin interval midpoint. To determine the environment encountered by the sharks, we constructed temperature-depth profiles from the transmitted PSAT data. As the temperature-depth data transmitted by the tags are quite sparse, temperature profiles along each track were constructed by applying a moving window of 72 hours to temperature-at-depth data transmitted by the tags. For data from each window, the depth-temperature relationship was interpolated from the surface down to the maximum depth within the window using a polynomial B-spline (bs() function in R, R Development Core Team 2011).

To determine the relative importance of diel vertical migration (DVM) and its plasticity through time, we compared the power of the 24, 12 and 6 hour periodicity for the complete time series of vertical movement from four tags that were recovered using wavelet analysis. Wavelet analysis is the local time-scale decomposition of a signal, which allows the estimation of the spectral characteristics of a signal as a function of time (Cazelles et al. 2008). Hence it does not assume stationarity of the signal, an assumption that needs to be addressed using ad hoc windowing procedures when using more traditional methods such as Fast Fourier Transform (Cazelles et al. 2008). Wavelet analyses using a Morlet wavelet transform were carried out in R using the 'biwavelet' package (Gouhier & Grinsted 2012).

Table 3.1 Dataset overview. Table showing details of the ten tagged broadnose sevengill sharks, days at liberty of tags, minimum straight line displacement and temperature range and maximum depth recorded by the tags.

ID	Sex	Total length (cm)	Mature	Deployment date	Days at liberty	Minimum straight line displacement (km)	Tag recovered	External temperature range (°C)	Maximum depth (m)
F1	F	233	Yes	10/05/2011	136	<10	No	8-13	50
F2	F	190	No	10/05/2011	136	<10	Yes	8.4-13	64
F3	F	152	No	10/05/2011	24	<10	No	11-13.2	48
F4	F	154	No	10/05/2011	13	54	No	11.6-13.8	56
F5	F	189	No	10/05/2011	135	96	Yes	11-14.4	360
M1	M	234	Yes	30/04/2010	153	891	Yes	12.75-18.2	209.5
M2	M	216	Yes	03/06/2009	94	887	No	11-16.6	192
M3	M	214	Yes	05/05/2009	29	356	No	12.4-16.4	280
M5	M	211	Yes	02/05/2008	51	708	No	11-15.6	208
M4	M	208	Yes	30/04/2008	47	424	Yes	11.6-15.2	175

Table 3.2 Data collection and summary set-up of the tags for the three deployment periods.

	2008	**2009**	**2010/2011**
Temperature bins	0; 5; 10; 12; 14; 16; 18; 20; 22; >22	10; 11; 12; 13; 14; 15; 16; 17; 18; 19; 20; 21; 22; >22	8; 9; 10; 11; 12; 13; 14; 15; 16; 17; 18; 20; 22; >22
Temperature sampling frequency	120 sec	120 sec	60 sec
Depth bins	0; 2; 10; 20; 40; 60; 80; 100; 150; 200; 300; 500; 700; >700	0; 2; 10; 20; 40; 60; 80; 100; 120; 150; 200; 250; 300; >300	0; 2; 10; 20; 40; 60; 80; 100; 120; 150; 200; 250; 300; >300
Depth sampling frequency	30 sec	10 sec	10 sec
Histogram summary period	24 hours	6 hours	6 hours
Deployment duration	180 days	138 days	138 days

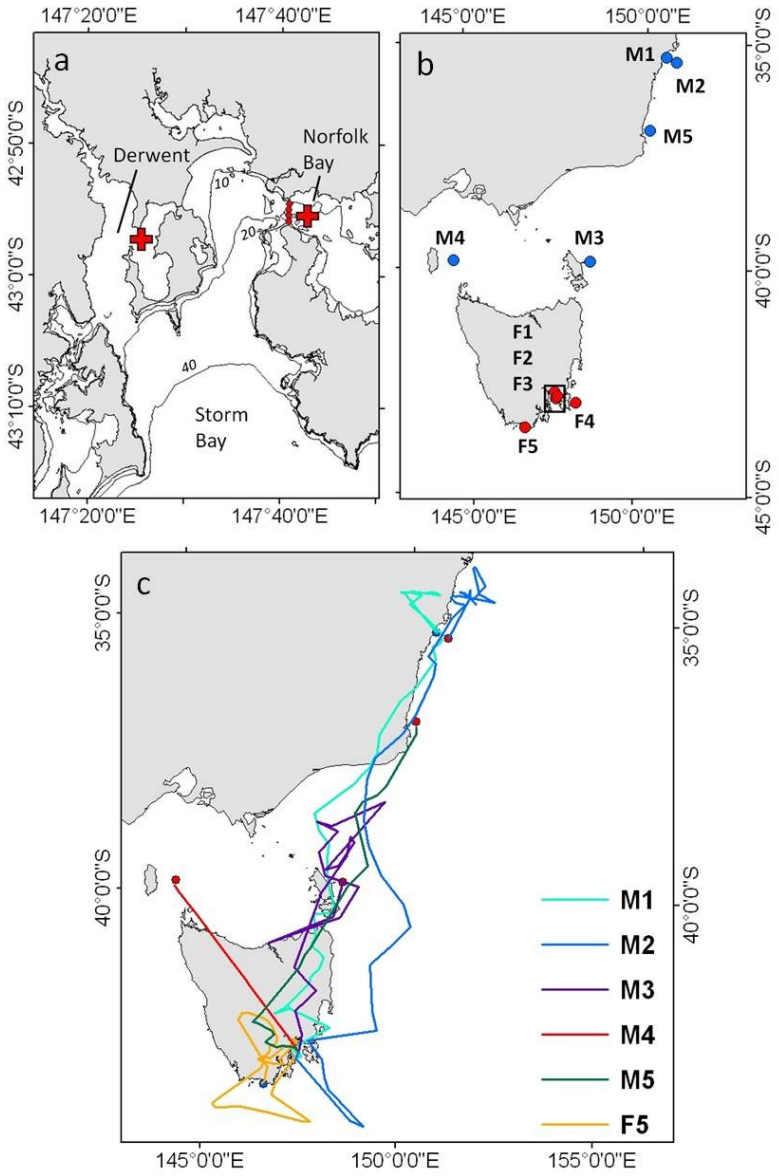


Figure 3.1 Map of **a)** the tagging locations in the Derwent Estuary/Norfolk Bay, **b)** satellite archival tag pop-up locations, **c)** most probable tracks estimated using Kalman filtering of raw geolocation data. In 3.1a, crosses indicate the two tagging locations, 10m, 20m and 40m contour lines are shown. Extent of the map is indicated by the black rectangle in Fig. 3.1b. In 3.1b, red circles indicate tags deployed on female sharks, blue circles indicate tags deployed on male sharks, tag IDs are displayed next to markers. In 3.1c, red circles indicate pop-up locations, coloured lines indicate most probable tracks. Only one female track is shown as all other females either did not leave the coastal tagging area or time at liberty was too short for track estimation.

3.3 Results

A total of 10 pop-up satellite archival tags were deployed on five male and five female broadnose sevengill sharks (Table 3.1). Tagged males ranged from 208 cm to 234 cm total length (TL), tagged females ranged from 152 cm to 233 cm TL. Male sevengill sharks mature at approximately 150-180 cm TL (Barnett et al. 2012b), which means all tagged males were adults. Females on the other hand grow larger than males and mature at approximately 220 cm TL, hence only one of the tagged females was considered an adult at the time of tagging. Mean time at liberty was 75 days for males (SD=50 days) and 89 days for females (SD=64 days) (Table 3.1). Out of the five tags deployed on male sharks, only one tag stayed on the shark for the programmed amount of time, with all other tags detaching prematurely. Out of the five tags deployed on females, three tags remained attached to the sharks for the programmed amount of time. Four tags, two deployed on males and two deployed on females were recovered after detachment (Table 3.1) and the complete data records were available for analysis.

3.3.1 Large-scale movement

All tags deployed on male sharks popped-up north of the tagging location, two in the Bass Strait and the remaining three off the east coast of mainland Australia (Fig. 3.1b), resulting in minimum straight line displacement of up to 890 km (Table 3.1). The two that popped-up in the Bass Strait were the males with the shortest time at liberty; these may have been en route further north to the east coast or west towards the central south coast of mainland Australia when the tags detached.

Three of the tags deployed on females popped-up in Norfolk Bay where they were deployed (IDs: F1, F2, F3), while the remaining two tags popped-up on the south-east coast of Tasmania (ID: F4) and the far south coast (ID: F5) respectively (Fig. 3.1b). Pop-up location of tags deployed on females did not appear to be influenced by time at liberty or maturity of the shark, as tags from both mature and immature sharks popped-up in Norfolk Bay and two of the tags that popped-up in Norfolk Bay as well as the tag that popped-up at the far south coast were attached for the complete deployment period of 136 days.

3.3.2 Temperature preferences

Differences in timing of emigration from the tagging location were evident in the sea surface temperature (SST) experienced by the tagged animals (Fig. 3.2). All tagged males moved into areas with higher SST than at the tagging location soon after tagging (Fig. 3.2a), but the timing of departure from the coastal areas, indicated by a downward shift in weighted mean depth at the beginning of the deployment period, varied between sharks (Fig. 3.3a). The coldest temperatures experienced by males were encountered while in the coastal waters for all males apart from individual M1 (Fig. 3.3a). However, the fact that minimum temperatures experienced ranged from 11 to 12.75°C (Table 3.1) and timing of departure varied even between animals tagged in the same year suggests that if changes in temperature caused the male sharks to leave, temperature thresholds differed between individuals.

In contrast to the males, SSTs experienced by tagged females were clearly split into two different groups (Fig. 3.2b). Despite the high short-term variability between June and

September most likely caused by high freshwater influx during the winter months, SSTs experienced by the three females whose tags popped-up at the tagging location (IDs: F1, F2, F3) closely followed monthly averages for the Derwent estuary (Fig. 3.2b). This suggests that while leaving the shallow Norfolk Bay (max depth 20 m) for deeper parts of the coastal system, these females did not leave the coastal areas over winter (Fig. 3.2b). Weighted mean depths above 50m throughout the deployment period for these three animals support this (Fig. 3.3b). These animals experienced the coldest temperatures of all tagged individuals with minimum temperatures as low as 8°C (Table 3.1) and spent approximately 80% of their time at or below the 10-12°C temperature bin (Fig. 3.4a). The two females whose tags popped-up away from the tagging location (IDs: F4, F5) moved into waters with much warmer temperatures throughout the water column soon after tagging (Fig. 3.3b). They most likely moved up the east coast of Tasmania where the influence of the East Australian Current causes water temperatures to be higher than in southern Tasmania. One of the tags popped-up there after 13 days at liberty (ID: F4) while the second tag (ID: F5) popped up off the south coast at the end of its deployment period (135 days). Movement into warmer waters by these females caused their cumulative distribution functions of time spent at a given temperature range to be closer to those of the males than those of the females that stayed in the coastal areas, with less than 10% of the time spent at or below the 10-12°C temperature bin (Fig. 3.4a).

3.3.3 Depth preferences

Despite the fact that females that stayed in the coastal areas over winter reached much shallower maximum depths than males or females that left the coastal areas (Table 3.1), their

cumulative distribution functions of time spent at a given depth range were relatively similar up to the 60% mark; both groups spent over 70% of their time at or above the 40-60m depth bin (Fig. 3.4b). For large parts of their tracks, the males and the females that left coastal areas showed similar mean swimming depths (around 20m) as females that stayed, yet, their mean swimming depth also dropped below 50 and 100 m on several occasions (Fig. 3.3). All sharks showed phases where mean depth was closer to the maximum depth reached and phases where mean swimming depth fell between the maximum depth and the surface (Fig. 3.3). This suggests that sharks shift between periods where they utilize large parts of the water column and more bottom oriented behavior.

Archival records for the four recovered tags showed that the sharks displayed consistent vertical movement, utilizing large parts of the water column (Fig. 3.5). Males however, displayed two distinct phases: a surface oriented phase characterized by consistent returns to the surface and a deeper swimming behavior, with no return to the surface for over 24 hours (Fig. 3.5a). During the shallow phase for male M1, diel vertical migration (DVM) was evident, with a strong 24 hour periodicity in vertical movement (Fig. 3.6), as the shark stayed near the surface for most of the night and at depths of 10 to 20 m during the day (Fig. 3.5a). During the deep swimming phase, it appeared to abandon DVM behavior, as the relative importance of the 24 hour periodicity was reduced and changes in depth were much less regular (Fig. 3.6). Male M4 on the other hand, displayed DVM during both the shallow and the deep phase (Fig. 3.5a), with the 24 hour periodicity being dominant throughout (Fig. 3.6). Female F2, which appeared to have remained in the shallow coastal areas, also displayed surface oriented phases as well as

phases during which it did not return to the surface for periods of more than 24 hours (Fig. 3.5b). DVM was evident during both deep and shallow phases for this individual as well (Fig. 3.5b), albeit with changes in the magnitude of depth variation (Fig. 3.6). The female that left the coastal areas (ID: F5), on the other hand, showed regular returns to the surface throughout its track but had phases of deeper and shallower vertical movement (Fig. 3.5b). Strong DVM behavior was evident throughout but particularly during the deeper phase (Fig. 3.5b). The shark returned to the surface every night, even after spending the day at great depths, making vertical movements of up to 360 m in a 24 hour period. In addition to DVM, all sharks with recovered tags showed an overall increase in vertical movement rate during nighttime with magnitude in vertical movement getting larger (Fig. 3.5) and maximum dive depths were reached at nighttime, between 17:40 and 03:32. External temperature records obtained from recovered tags showed very little temperature variation with depth for sharks M4 (Fig. 3.5a) and F5 (Fig. 3.5b), even as the sharks dove to depths in excess of 100m, indicating a relatively well mixed water mass. Shark M1 on the other hand experienced considerable variation in temperature during its deep phase, with temperature decreasing with increasing depth (Fig. 3.5a). However, there was no regular pattern in the shark's vertical movements and corresponding variations in external temperature. Shark F2 also experienced considerable temperature variations during its deep phase, yet, in this case, coldest temperatures were experienced during sporadic ascents close to the surface (Fig. 3.5b), indicating the presence of a colder surface layer.

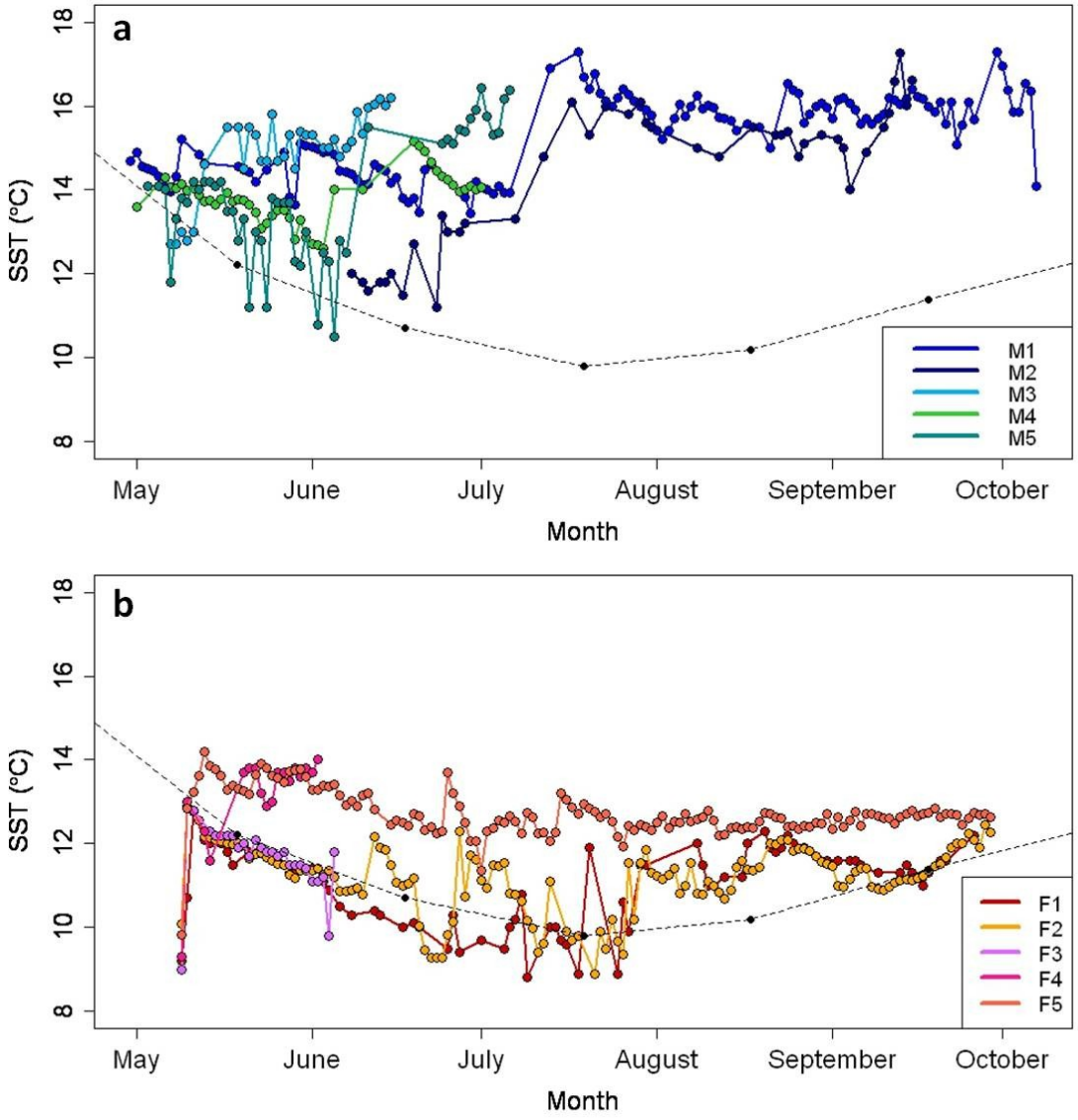
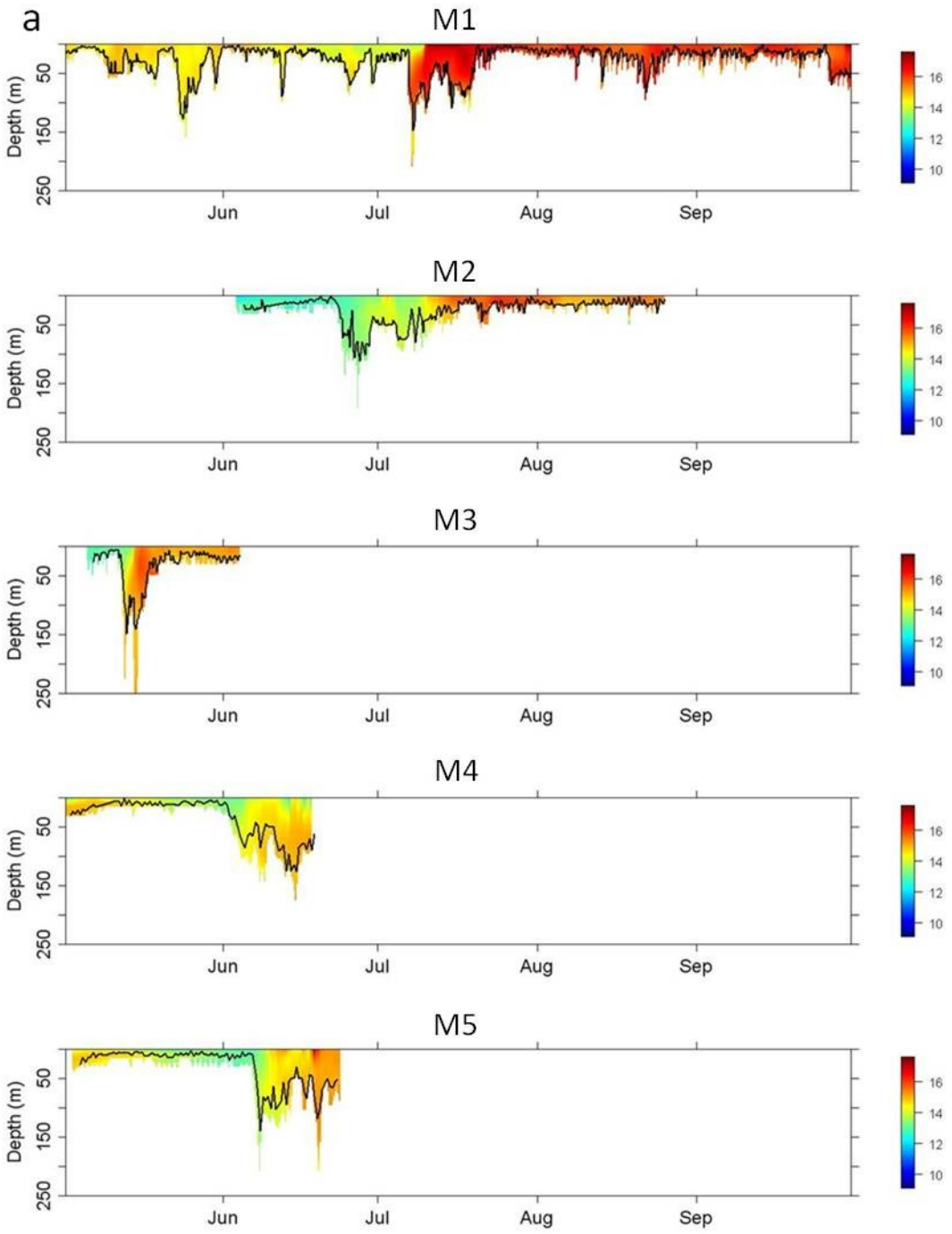


Figure 3.2 Sea surface temperature (SST) encountered by individual **a)** male and **b)** female sharks during the PSAT deployment period. SST was defined as any temperature measured by the tags above 5m depth. Females F1, F2, F3 remained in the coastal areas during their time at liberty, females F4, F5 left the coastal areas. The black dashed line indicates monthly SST averages for 4 stations at the entrance to the coastal embayment where sharks were tagged. Monitoring data was obtained from the Derwent Estuary Program.


a
M1
M2
M3
M4
M5
Depth (m)
50
150
250
Jun
Jul
Aug
Sep
16
14
12
10

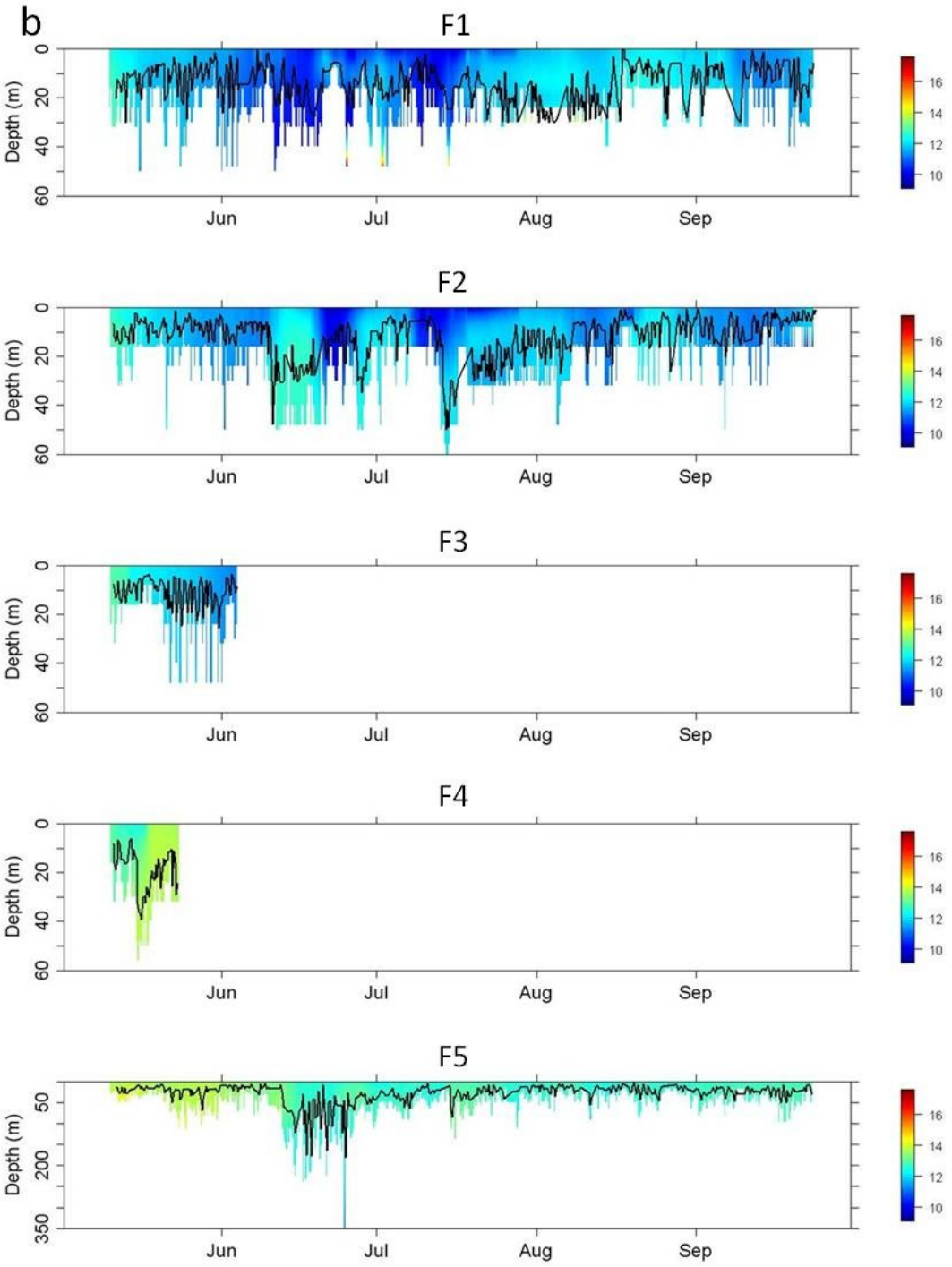


Figure 3.3 Weighted mean swimming depth (black line) and interpolated temperature/depth profiles for **a)** 5 tagged male sevengill sharks and **b)** 5 tagged female sevengill sharks.

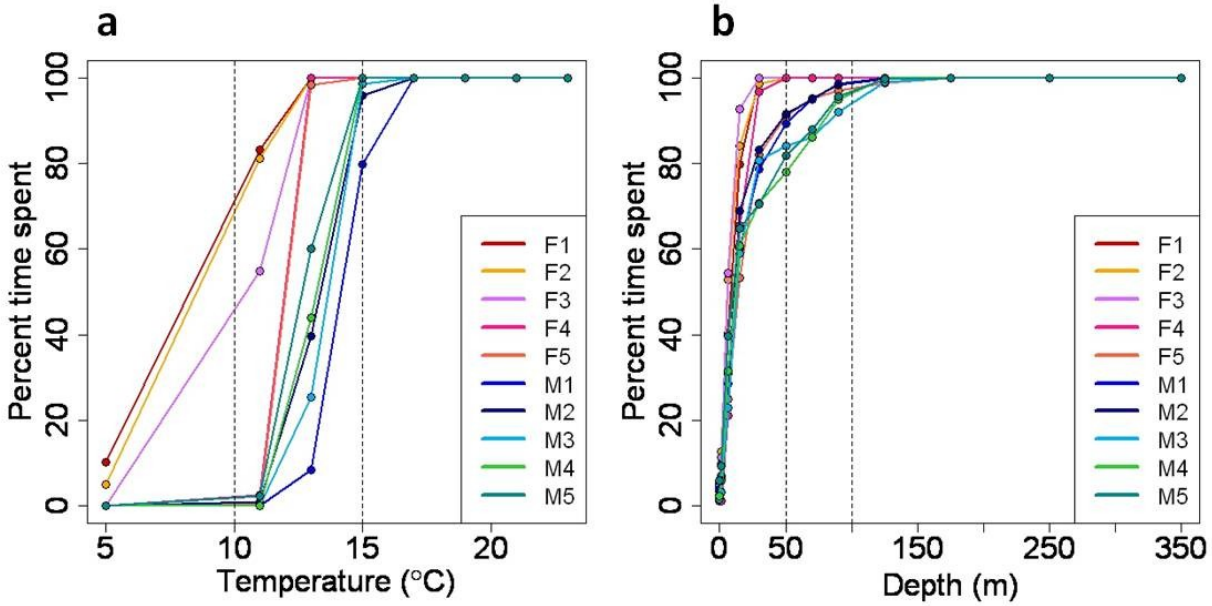
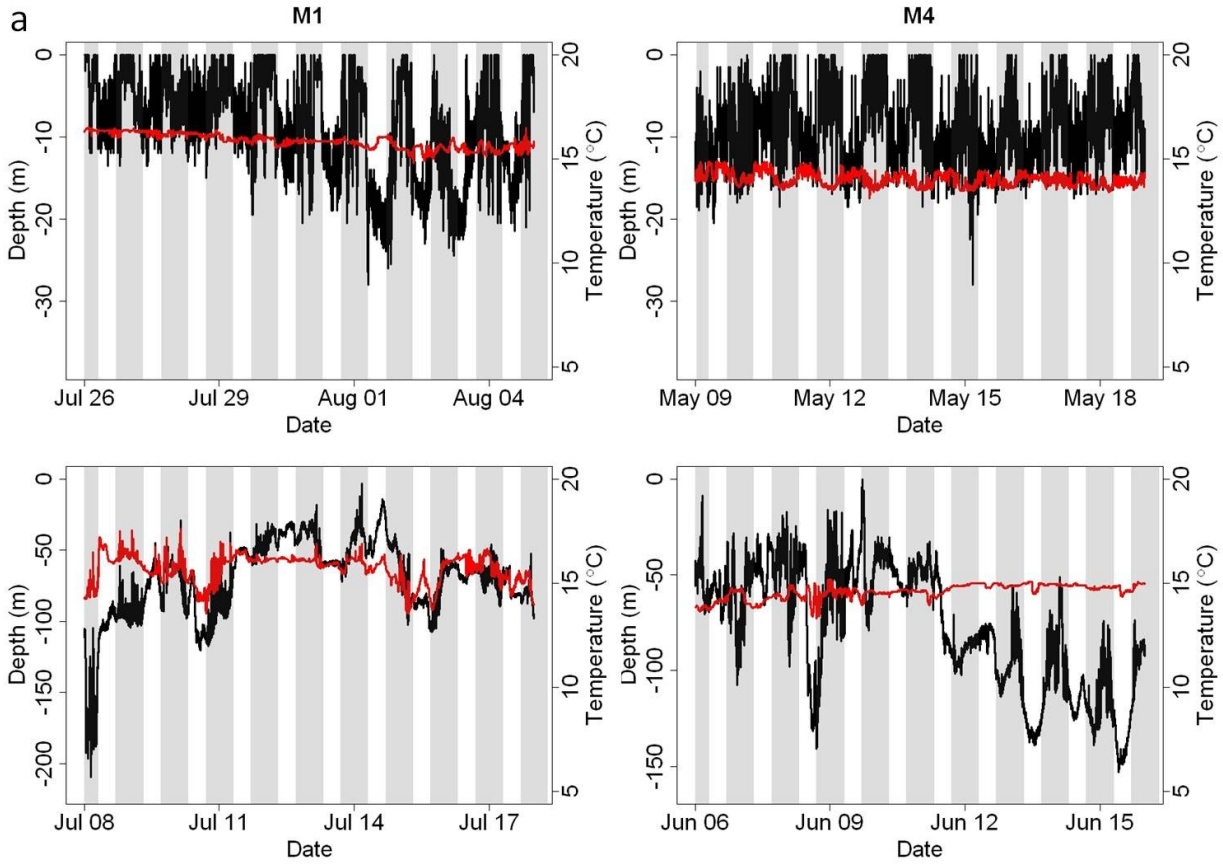


Figure 3.4 Cumulative distribution function of time spent at **a)** temperature bins and **b)** spent at depth bins outlined in Table 3.1. Bins were standardized across tags and the center of the standardized bins used for plotting.


a
M1
M4
Depth (m)
Temperature (°C)
Date
Jul 26
Jul 29
Aug 01
Aug 04
May 09
May 12
May 15
May 18
Jul 08
Jul 11
Jul 14
Jul 17
Jun 06
Jun 09
Jun 12
Jun 15

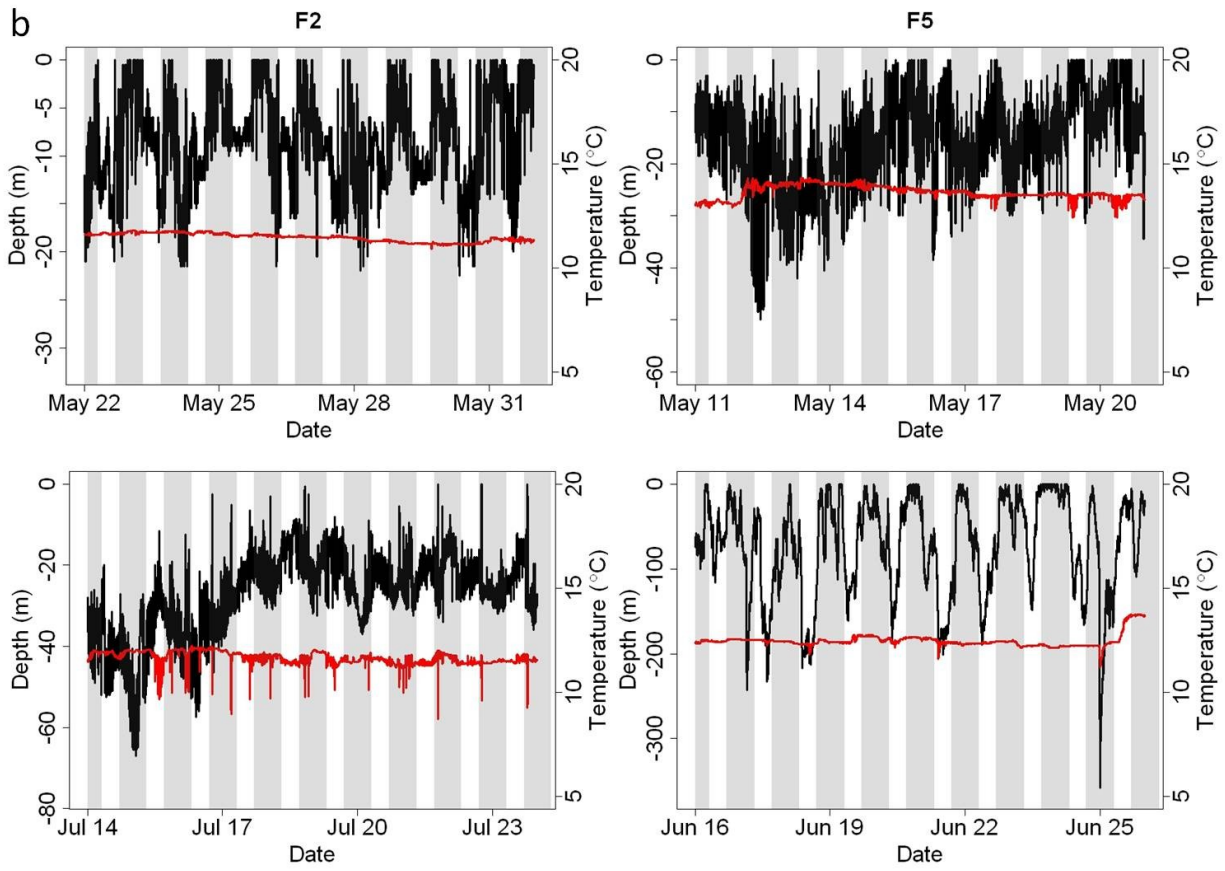


Figure 3.5 Vertical movements for two 10 day periods from **a)** two male and **b)** two female broadnose sevengill sharks. One of the females left the coastal areas over winter (ID: F5) and one stayed (ID: F2). Top panels show 10 day example of depth (black line) and external temperature level (red line) during shallow swimming phases, bottom panel shows 10 day example of depth and external temperature during deep swimming phases. Vertical grey bars represent nighttime periods from sunset to sunrise, including nautical twilight.

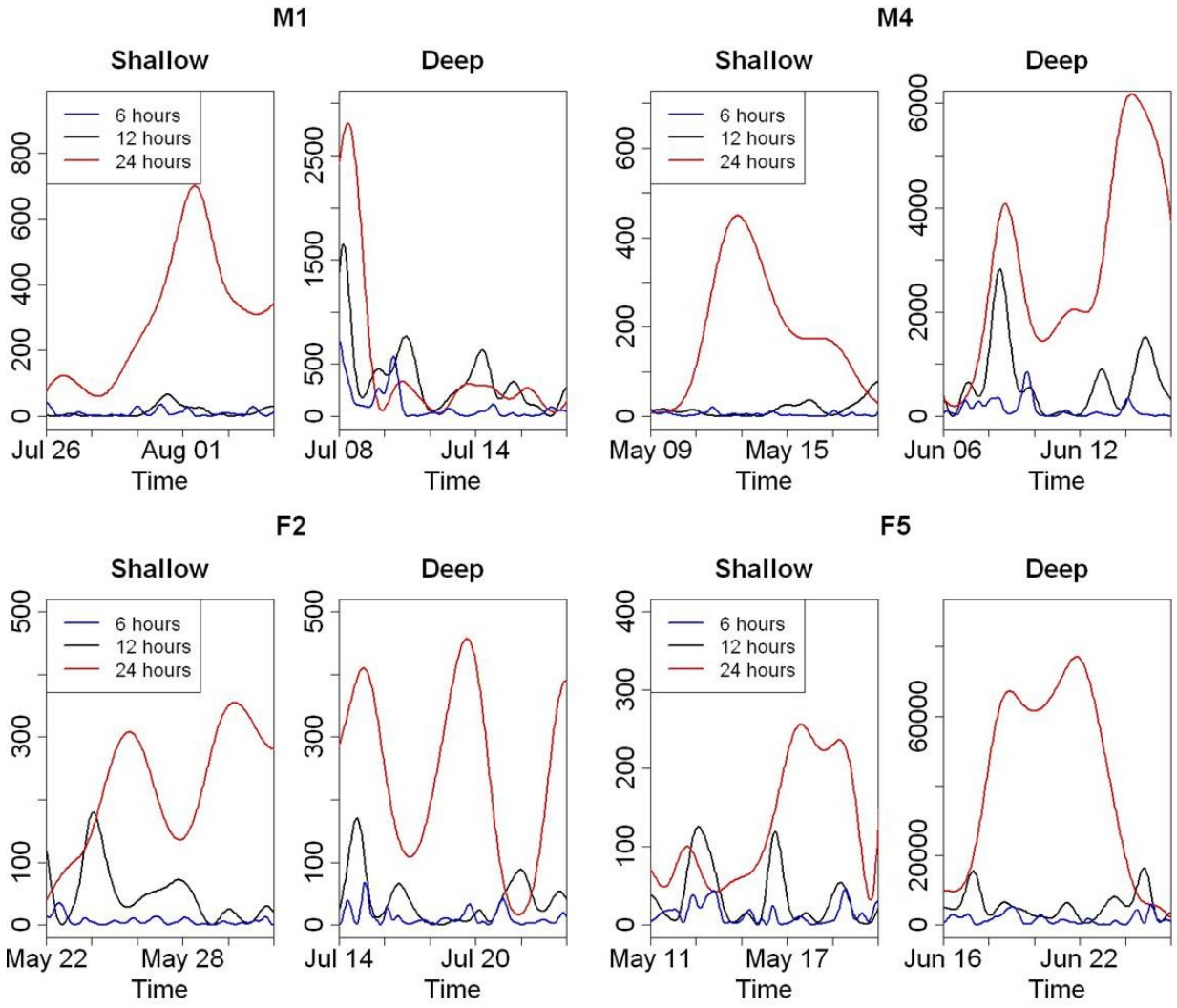


Figure 3.6 Change in power over time for the 6, 12 and 24 hour periodicity in swimming depth for the example periods of shallow and deep swimming phases in Fig. 3.5, determined using wavelet analysis of mean hourly swimming depth from recovered archival tags. Absolute power is dependent on the magnitude of the oscillation. Hence, scales are much larger for deep than for shallow periods. Where the 24 hour periodicity is strongest in the signal, relative to the 12 and 6 hour periodicities, diel vertical migration (DVM) is the dominant behavioural mode.

3.4 Discussion

This study has provided new insight into the migratory behavior and vertical movements of a relatively poorly studied temperate shark species of great ecosystem importance. We found behavioral differences in the winter migration of male and female broadnose sevengill sharks tagged in Tasmania. All males left coastal areas between mid-May and the end of June to move northwards into warmer waters, covering minimum distances of up to 880 km. Some of the females remained in the coastal system for the entire winter, in waters with temperatures as low as 8 °C, while others left coastal areas and moved into deeper and warmer waters offshore. Females that remained in coastal areas left Norfolk Bay and moved into deeper parts of the coastal system, possibly into Storm Bay, which has been suggested to be the winter habitat of juvenile school sharks *Galeorhinus galeus* (Stevens & West 1997), an important prey species for sevengill sharks (Barnett et al. 2010a).

These results further support both sex specific and within female differences in migratory patterns previously proposed for sevengill sharks in Tasmania from acoustic tracking and stable isotope analysis (Abrantes & Barnett 2011, Barnett et al. 2011). Sex specific differences in long-distance movement in the sevengill shark were also detected in animals tagged in the Pacific Northwest of the USA. However, in that region roles appeared to be reversed, with long distance coastal movements into warmer waters carried out by female sharks (Williams et al. 2012). Sex specific differences in seasonal migration could be due to one or a combination of

differences in thermal tolerance, seasonal and/or spatial resource partitioning or reproduction (Springer 1967, Wearmouth & Sims 2008).

Migrations driven by changes in water temperature have been reported for numerous shark species (Speed et al. 2010). It is possible that the sexual dimorphism in the bodysize of sevengill sharks might cause sex specific differences in thermal tolerance, as has previously been reported for other elasmobranch species (Wallman & Bennett 2006), with the larger females being able to withstand lower temperatures. However, the study from the West coast of the USA, where the migratory pattern for males and females was reversed seems to contradict this hypothesis (Williams et al. 2012). Further deployments of archival tags in different parts of this species' range are required to better understand the thermal tolerances of male and female sevengill sharks.

It is also possible that differences in migratory behavior are due to seasonal resource partitioning, caused by diminished foraging resources in winter, when the main chondrichthyan prey species are absent from coastal areas (Barnett et al. 2010c). Intraspecific differences in seasonal migration driven by resource partitioning have been shown for various ungulate species such as the Yellowstone pronghorn *Antilocapra americana* (White et al. 2007) and moose *Alces alces* (Ball et al. 2001) and tend to emerge when migrants and non-migrants in a population receive approximately equal payoffs (Swingland & Lessells 1979).While differences in migratory behavior in those species were not sex specific, it is possible that the sexual dimorphism in body size of sevengills can lead to sex specific resource partitioning. In order to reach the body size required for gestation of embryonic young, females may have greater

energetic demands than males, leading to the evolution of differential migration, as has been suggested for the scalloped hammerhead shark *Sphyrna lewini* (Klimley 1987). Another possibility is that males are competitively inferior due to their smaller body size and are forced to leave to seek new foraging opportunities, a common phenomenon in seasonal partial migrations (see Chapman et al. 2012 for review). Both of these hypotheses require the assumption that it is energetically advantageous for the females to remain in coastal areas over winter, with males being forced to pay the cost of migration due to the diminished prey resource.

The most common driver of sex specific migrations in sharks, however, is generally thought to be the difference in reproductive requirements of males and females (Sims et al. 2001). In contrast to sevengill shark populations in Argentina and California (Ebert 1989, Lucifora et al. 2005), sevengill sharks in Tasmania do not appear to use the coastal areas as pupping grounds or nursery areas, as neonates are not present in these areas (Barnett et al. 2010c). Moreover, Barnett et al. (2010c) failed to detect any fresh mating scars on female sevengill sharks in the coastal area, indicating that it is not used for mating either. It therefore has to be assumed that both mating and pupping occur outside of the Tasmanian coastal areas.

The areas on the east coast of mainland Australia frequented by the tagged males are unlikely to be used for mating, however, as sevengill catches in shark control beach nets in NSW are overwhelmingly male (Barnett et al. 2011). Hence, Barnett et al. (2011) hypothesized that mating may occur at the entrance to the Derwent estuary in autumn, prior to the males

northward migration, suggesting that large-scale movement behavior of males is not driven by reproductive requirements. Long-distance movements by the females on the other hand may be driven by reproductive requirements, as migrations to pupping grounds in warmer waters have previously been reported for other shark species (e.g. porbeagle shark *Lamna nasus,* Campana et al. 2010) and have been suggested for female sevengill sharks in the Pacific Northwest of the USA (Williams et al. 2012). The biennial reproductive cycle of sevengill sharks (Ebert 1989) would hereby explain why only some of the tagged females left and others remained at the coastal site. However, based on length at maturity data from other regions (Barnett et al. 2012b), four out of the five females tagged in this study have to be considered subadults and the natal sites are not known for the Tasmanian population. Hence, the link between reproductive and migratory behavior cannot be established from this study.

Whatever the reason for the differences in migratory behavior, it potentially has significant ramifications for the management of this species, as males and females are likely to be subject to different rates of fishing mortality during the winter. Neither sex spent large amounts of time in the designated protected areas in Tasmanian coastal waters, although females do so more than males (Barnett et al. 2011). Outside of these areas, fishing pressure is unlikely to be uniformly distributed between southern Tasmania and the east coast of Australia. This may cause differential exploitation of the sexes, as has been suggested for the shortfin mako *Isurus oxyrinchus* in the South Pacific (Mucientes et al. 2009).

In contrast to horizontal movement, there were few differences in the characteristics of vertical movements between male and female sevengill sharks. Both sexes displayed diel vertical migration (DVM) throughout much of their tracks and spent more time at or near the surface at night and more time at depth during the day. This behavior is relatively common in sharks (Speed et al. 2010) and is generally linked to predator avoidance (Enright & Hamner 1967), thermoregulation (e.g. Carey et al. 1990, Sims et al. 2006) or foraging (e.g. Nakano et al. 2003). Since sevengill sharks have few potential predators, predator avoidance is unlikely to be the driver of DVM behaviour. And since archival records showed that DVM behavior was evident in well-mixed water masses, with relatively homogeneous temperatures, thermoregulation can also be discounted as the reason for vertical migration. Hence, foraging is the most likely driver of DVM for sevengill sharks in Tasmania. Similar to the bluntnose sixgill shark *Hexanchus griseus* (Andrews et al. 2009), Greenland shark *Somniosus microcephalus* (Stokesbury et al. 2005) and Pacific sleeper shark *Somniosus pacificus* (Hulbert et al. 2006), this behavior became less pronounced as male sharks moved offshore into deeper waters. This may be due to sharks switching to a different foraging strategy when in transit mode or feeding on different prey species with different vertical movement behavior.

The female that left the coastal areas for deeper offshore areas on the other hand showed persistent DVM throughout, with large diel changes in swimming depth and vertical movements to depths of up to 360 m. This is the deepest record reported for this species and if linked to foraging behavior could mean potential resource overlap between sevengills and

deep-water shark species of the same order such as the bluntnose sixgill shark and the sharpnose sevengill shark *Heptranchias perlo*, (see Barnett et al. 2012b for review of this topic). The female sevengill sharks that remained in the coastal areas displayed DVM for the entire winter period albeit with changes in the diel depth range and mean depth. These changes might be due to movement in and out of shallower areas or changes in either nighttime light intensity through cloud cover and lunar phases, as has been reported for school sharks (West & Stevens 2001) and juvenile white sharks (Weng et al. 2007) or surface temperature and salinity through increased freshwater flow at the surface. The possible influence of surface temperature is supported by the fact that one of the sharks reduced its nightly returns to surface waters in the coastal area to sporadic, short ascents when the surface layer was considerably cooler than the water underneath.

In addition to DVM, sevengill sharks also showed a diel change in vertical movement rate with vertical movement increasing in magnitude during the night. This nightly 'yo-yoing' behavior has previously been reported for this species from acoustic tracking data in shallow habitats (Barnett et al. 2010b) as well as for other shark species (e.g. Heithaus et al. 2002, Andrews et al. 2009). It may be used to detect olfactory cues in the water column and/or ambush prey in low light conditions (Carey & Scharold 1990, Barnett et al. 2010b), to reduce energetic cost of travel by switching between energy efficient gliding during descents and active swimming during ascents (Weihs 1973) or to detect magnetic gradients as a means of navigation (Carey & Scharold 1990). As sevengill sharks exhibited yo-yoing behavior throughout their tracks, in both shallow and deep water and during both resident and transit phases it is likely to be primarily

employed as a foraging strategy as has previously been reported for tiger sharks *Galeocerdo cuvier* (Nakamura et al. 2011), where it was also attributed to foraging. If this is the case, it suggests that sevengills foraged throughout their tracks, rather than switching between commuting and foraging modes as has been reported for other marine species such as leatherback turtles (James et al. 2005) and salmon sharks (Weng et al. 2008). Hence, migratory behavior did not seem to include a suppression of responses to foraging resources as Dingle (1996) suggested. While this type of behavior has been described as ranging rather than migrating for other species (Kuhn et al. 2009), the strong fidelity of sevengill sharks to their summer feeding sites in Tasmanian coastal areas (Barnett et al. 2011) means that their movement most likely falls somewhere between the two.

As the first comprehensive analysis of pop-up satellite archival tag data from broadnose sevengill sharks, this study shows the complexities of the movement behavior of this important apex predator, complexities the species shares with numerous other shark species and that need to be understood if successful management is to be achieved (Speed et al. 2010).

Chapter 4 - Quantifying coastal shark movement behaviour from acoustic telemetry data: Sex specific differences in space-use of the broadnose sevengill shark

4.1 Introduction

Movement is a prominent yet poorly understood behavioral activity (Patterson et al. 2008), exerting fundamental influence on the distribution patterns and temporal dynamics of many animal populations (Bowler & Benton 2005). Movement patterns generally emerge through the interplay between an individual's internal motivation for movement and external factors (Nathan et al. 2008), such as habitat, which includes physical (Morrissey & Gruber 1993), chemical (Brill 1994) and biological (Sims et al. 2005) parameters and interactions with conspecifics, which includes mating (Pratt & Carrier 2001), competition (Jones 1987) and schooling (Newlands et al. 2006). Understanding the link between these external variables and animal space-use patterns is challenging but fundamental to developing effective management and conservation measures (Nathan et al. 2008) in the face of habitat loss and fragmentation, particularly in coastal areas such as bays and estuaries (Speed et al. 2010).

In the marine realm, the use of automated acoustic tracking has become an exceedingly popular and affordable research tool for monitoring the movement of highly mobile, free-ranging animals in coastal and continental shelf areas (Heupel et al. 2006). However, the development of quantitative methods for analysing patterns of space-use from automated acoustic array data has lagged behind the technological advances in the field (Sims 2009).

The application of social network analysis has recently emerged as a promising tool for extracting quantitative information on spatio-temporal co-occurrences of individuals from fixed acoustic array data, improving our understanding of the link between aggregating behavior and individual movement (Stehfest et al. 2013). Additionally, spatial network analysis has been proposed as a tool for analysing frequencies of movement between receivers from acoustic detection sequences to quantify individual differences in space-use and determine the influence of habitat on movement patterns (Jacoby et al. 2012). However, by only using transition counts as the basis for movement analysis, the proposed method ignores temporal information on transition durations and residency periods, providing a potentially incomplete picture of movement patterns.

Stochastic models which treat transitions between states as a Markovian process, i.e. a process in which the probability of moving from one state to the next is only dependent on the present state, have been used to explore and simulate a vast range of dynamic systems from meteorological phenomena (Jimoh & Webster 1996) to the large-scale movement of animals (Eveson et al. 2009). One of the important characteristics of Markov chains is that if the chain does not contain absorbing states (i.e. the transition probability from a given state to itself is less than 1 for all states), it is possible to determine the equilibrium state of the Markov chain. This is the probability of being in a given state after a large number of time steps, regardless of the starting state. This characteristic has been used in a variety of applications such as the

succession of species in rocky subtidal communities (Forrest Hill et al. 2004) and in its most prominent form to rank webpages in internet search engines (Langville & Meyer 2005).
In this chapter, I applied both social and spatial network analysis as well as Markov chain modeling to fixed receiver acoustic tracking data for the broadnose sevengill shark (*Notorynchus cepedianus*), a large (up to 3m) demersal shark of the order *Hexanchiformes* (Barnett et al. 2012b).

Sharks, which are often slow growing, late maturing and have low fecundity, are considered highly vulnerable to overexploitation (Compagno 1990) and the global decline in their abundance and the potential ecosystem-wide ramifications are a growing concern among fisheries scientists (Heithaus et al. 2008, Estes et al. 2011). Coastal shark populations are particularly affected by disturbance to their natural habitat due to their close proximity to human populations (Holland et al., 1999). Additionally, a number of shark species (e.g. scalloped hammerhead, Klimley 1987, basking shark, Sims et al. 2000) display sex-specific aggregating behavior (see Jacoby et al. 2011). In some cases, such as the basking shark population in the north-eastern Atlantic, this has led to differential exploitation of the sexes, resulting in a dramatic decline in the population (Sims et al. 2000). Hence, improving our understanding of individual-habitat and between-individual interactions is essential for the development of successful conservation and management measures (Speed et al. 2010) and a multitude of studies have employed acoustic tags and fixed arrays of acoustic receivers to achieve this (see Sundström et al. 2001, Sims 2009, for review). However, only few of these

studies (e.g. Levin et al., 2012) have gone beyond the analysis of frequency of detections at individual receivers (Jacoby et al. 2012).

The broadnose sevengill shark is one of the most important apex predators in temperate coastal areas around the world (Last & Stevens 2009), due to the high diversity of its diet, which includes marine mammals, chondrichthyans and teleosts (Cortés 1999, Barnett et al. 2010a). While not a target species, it is often caught as by-catch in commercial shark fisheries (Compagno 1984) and targeted by recreational fishermen (Lucifora et al. 2005). Despite its importance as an apex predator in coastal marine systems, until recently little was known about the species' ecology beyond dietary information (Ebert 2002, Braccini 2008, Barnett et al. 2010a) and it is therefore listed as data deficient on the IUCN Red List (Fowler et al. 2005). However, a number of recent studies carried out in Patagonia (Lucifora et al. 2005), the west coast of the USA (Williams et al. 2011) and Tasmania (Barnett et al. 2010c) (Chapter 3) have shed light on their large-scale movement and the structure and seasonal dynamics of the respective populations. The studies showed a marked increase in abundance in coastal areas in spring and summer, followed by a near absence in winter and individuals have been shown to display strong site fidelity in their return to certain coastal sites after winter. In Patagonia (Lucifora et al. 2005) and California (Ebert 1989), seasonal aggregations in coastal areas have been attributed to pupping activity, whereas prey abundance was considered the main factor driving the seasonal use of coastal areas in Washington State (Williams et al. 2011) and Tasmania (Barnett et al. 2010c).

Additionally, two fixed array acoustic tracking studies in Tasmania (Barnett et al. 2010b, Barnett et al. 2011) and Washington State (Williams et al. 2012) have determined the fine-scale movement behaviour and seasonal habitat-use patterns of these animals during their residency in coastal areas. While providing valuable insight into the sharks' space-use, neither study went beyond the analysis of detection frequencies at individual receivers and the information on residency periods and connectivity between habitats held within the acoustic tracking data was not fully exploited.

I used acoustic tracking data from male and female broadnose sevengill sharks, collected by Barnett et al., (2010) in a system of coastal embayments in South East Tasmania to test the suitability of the methods outlined above for analysing fixed array acoustic tracking data and determine whether the sex-specific differences in large-scale movement behaviour described in chapter 3 are also evident in the sharks' coastal movement. In this chapter the analysis proceeded as follows

1) Social network analysis was employed to quantify spatially and temporally explicit co-occurrences between tagged individuals and test for sex specific aggregating behaviour
2) Spatial network analysis of between-receiver transitions was carried out to determine differences in space-use between male and female broadnose sevengill sharks in the coastal areas and identify preferred areas within the shark refuge areas.

3) Temporally explicit, stochastic models were applied to the acoustic detection sequences to determine differences in space-use between males and females and identify preferred areas.
4) Pattern oriented modeling (POM), i.e. simulating from an empirically estimated model and then assessing whether the simulations accurately reproduce patterns observed in the data (Grimm et al. 2005, Vinatier et al. 2011) was used to assess the suitability of the stochastic modelling approach for analysing movement from acoustic tracking data.

4.2 Materials and methods

4.2.1 Data collection

An array of 72 acoustic receivers (VR2 receivers, VEMCO Ltd, Halifax, Canada) was deployed and continuously maintained for the period from December 2007 to June 2009 in the Derwent Estuary/Norfolk Bay, a system of coastal embayments on the south-east coast of Tasmania, Australia (Fig. 4.1). The Derwent Estuary runs through the City of Hobart before opening into Storm Bay, and consistently reaches depths of 20–30 m, with a maximum depth of 44 m. Norfolk Bay is a relatively shallow (average depth 15 m; maximum depth 20 m), semi-enclosed bay with an area of 176 km^2. Substrate in both areas is relatively homogeneous, consisting primarily of sand and silt with only a few small vegetated areas, dominated by seagrass and green algae from the genus *Caulerpa*.

Acoustic receivers can detect uniquely coded VEMCO acoustic transmitter tags when within detection-range of the receivers (approximately 400 to 500 m in this study as determined through range testing). The acoustic array was set up as single curtains and gates, with detection ranges of adjacent receivers overlapping so that sharks could be detected moving across and between entrances and choke points of the coastal areas. At choke points where the distance between shorelines was less than the detection range diameter, a single receiver was placed halfway between the shorelines. Since the study area encompasses shark refuge areas, in which no sharks, skates or rays of any kind may be taken (Tasmanian Department of Primary

Industries, Parks, Water and Environment), receivers were deployed along the boundaries of the protected areas to determine the residence of *N. cepedianus* in these areas (Fig. 4.1). Sharks were caught on bottom-set, baited longlines, lifted onto the tagging vessel with the aid of a cradle and turned on their back. When on their back, broadnose sevengill sharks enter tonic immobility which means that the sharks could be handled without the need for restraining. Aboard the tagging vessel, the hook was carefully removed from the shark's mouth, their eyes covered with a wet cloth to avoid injury, their sex identified and total length measured. The acoustic-coded V16 transmitters (90 mm length × 15 mm diameter; <1% of the animal's body weight, battery life >2 years, VEMCO Ltd.) were implanted into the peritoneal cavity via a 1–2 cm incision in the abdominal wall and the incision closed with surgical sutures. Aseptic techniques were used during surgery and the entire procedure lasted approximately 3-5 minutes after which sharks were lowered back into the water. Running seawater was continuously pumped over the gills of the shark throughout the procedure. Prior to release, a povidone-iodine antiseptic was applied to the wounds to aid healing. All methods used were approved by the University of Tasmania Animal Ethics Committee (No. A0009120).

Sharks were tagged during two periods, between December 2007 and March 2008 and between October and November 2008. Tagging in the Derwent Estuary was conducted in area 1 and between areas 1 and 2. Tagging in Norfolk Bay was carried out between areas 6 and 7 (Fig. 4.1). The final dataset consisted of 40 sharks. Male sharks ranged in size from 164 cm to 246 cm total length, females ranged from 153 cm to 284 cm. Previous studies have reported that males

mature at 150–170 cm total length and females mature at 210–220 cm total length (Ebert 1989, Ebert 1996, Lucifora et al. 2005).

4.2.2 Data processing

Prior to analyses, any false detections were removed from the dataset. False detections can occur due to acoustic signal collision; if an acoustic receiver receives the signals of two fish simultaneously, the two colliding signals may overlap and be recorded as the signal of another tag, leading to the false detection of a fish which is not within receiver range. These false detections were identified and removed in a two-step process. Firstly, all single detections with no additional detections within 1 hour before or after were removed from the raw dataset. Secondly, I calculated straight line velocity for each transition between successive detections at different receivers and identified any transitions that occurred at a speed greater than the largest recorded burst swimming speed for this species (6.1 m /s, Barnett et al. 2010b). I then manually assessed whether the start or end point of these transitions was the false detection, based on the animal's previous and subsequent detection sequence and removed them accordingly.

Prior to analysis, detections were aggregated both temporally and spatially. Temporal aggregation was required to reduce the size of the raw dataset (486096 records) to bring computation times to acceptable levels and because there is only limited information in large numbers of detections at the same receiver over a short period of time. Since animals were detected at multiple adjacent receivers within a given half hour, spatial aggregation of receivers

was necessary, as both network and Markov chain analysis require that each detection record can be assigned to a single group or state within the given time step. The smallest technically feasible time step was half-hourly; the resulting highest spatial resolution was that of receiver curtains. This resulted in 8 groups of receivers, henceforth referred to as *spatial states* (see Fig. 4.1 for map) where observations of a shark's presence were possible and further "dummy" states for regions where receivers were absent. These dummy states were allocated to the observation series during time periods when the animal was not detected at receivers. How these were constructed varied between approaches and is detailed below.

4.2.3 Social network analysis

To determine the frequency of spatio-temporal co-occurrences between pairs of tagged sharks and quantify the level of shared space-use, I employed the approach adapted from social network analysis as described in chapter 2 of this thesis. To briefly recap, the simple ratio index (SRI) of association was computed for each dyad of tagged sharks, based on common detections at receiver groups within a half hourly sampling period. The SRI was also computed for a 12 hourly sampling period to determine the level of shared space-use at a coarser temporal scale.

To test whether shared space-use between individuals differed significantly from randomness at the 2 temporal scales, I determined if there was a significant difference between real association patterns and those obtained from a large number of random permutations, which were computed as developed by Whitehead (2008) and described in chapter 2. To test whether

there were any differences in space-use or active avoidance behaviour between males and females, the permutation test was also carried out for only associations between male and female sharks.

4.2.4 Spatial network analysis

In addition to analysing shared space-use between individuals, network analysis can also be applied to determine patterns of directed movement between locations (Jacoby et al. 2012, Stehfest et al. 2013). In this case spatial locations, rather than individuals are the nodes in the network and the connections between them are counts of directed movement. Applying network analysis to such a movement network allows the identification of preferred areas and/or differences in space-use between males and females to be determined. To construct the movement network from the dataset of acoustic detections, two square matrices containing counts of movements between states (**M**) were computed; one for male and one for female sharks. Therefore the individual entries m_{ij}= the total number of movements between states *i* and *j* for the given sex, with movement between *i* and *j* defined as any instance of a detection in state *i* followed directly by a detection at state *j*, regardless of the time difference between the two detections. Treating the states as nodes and the counts of directed movements as weighted edges between them, two network metrics of centrality which are commonly used in network analysis and are described in detail below were calculated from the movement count matrices. Network metrics were also calculated for the adjacency matrix **A** of the movement network. This is a matrix defining (in this case geographic) accessibility. Therefore a_{ij}=1 if direct movement between states *i* and *j* is possible and a_{ij}=0 if it is not. This

adjacency matrix is equivalent to a matrix of movement counts in which every geographically possible movement occurs with the same frequency and hence represents the null model for the movement network to which the real movement network can be compared. The chosen network centrality metrics calculated for the movement and adjacency matrices were Degree centrality (Freeman 1979) and Eigenvector centrality (Newman 2004). These are defined as follows:

Degree centrality is a direct measure of the connectedness of each state in the spatial network. For a given state *i*, degree centrality ($C_D(i)$) is computed as the number of states that are connected to state *i* through direct movement, divided by the total number of states minus 1. Hence, for the movement matrices (**M**) for example, it is the number of elements (N) in the i^{th} row that are greater than 1, divided by the total number of elements minus 1.

$$C_D(i) = \frac{N(m_{i*} > 1)}{N(m_{i*}) - 1}$$

Eigenvector centrality, also called Gould's index of accessibility (Gould 1967), is a measure not only of the centrality of a state, but also of the centrality of the states it is connected to. It is computed as the dominant eigenvector (i.e. the eigenvector with the largest eigenvalue) of the movement network or adjacency matrix. An eigenvector of the square movement matrix **M** is a non-zero vector **v** which satisfies the equation $\mathbf{Mv}=\boldsymbol{\lambda}\mathbf{v}$, where $\boldsymbol{\lambda}$ is the corresponding eigenvalue, i.e. it is a non-zero vector which, after being multiplied by the matrix, remains proportional to the original vector. For any given square matrix a number of eigenvector/eigenvalue pairs exist.

However, the Perron-Fobenius theorem (Meyer 2000) states that for a matrix **M** which is both nonnegative (i.e. $m_{ij} \geq 0$ for all i,j) and primitive (i.e. there exists an integer $N>0$ for which all elements of $\mathbf{M}^N$ are positive[1]) a largest eigenvalue exists, which has a corresponding unique eigenvector with all positive entries, called the dominant eigenvector. This dominant eigenvector is equivalent to the vector of normalized row sums of the k^{th} power of the matrix, as k approaches infinity. From network theory we know that it is the weighted or unweighted proportion of the total number of paths in a network emanating from a given node (Newman 2004). To illustrate, the row sums of the 2^{nd} power of a network matrix are equal to the total number of paths of step length 2 from each node. Accordingly, the row sums of the k^{th} power of the network matrix are equal to the total number of paths of step length k from each node. As k approaches infinity, the normalized vector of row sums converges to a steady state – the dominant eigenvector. The dominant eigenvector was estimated using the power method, an iterative method where the network matrix is multiplied by an initial guess of the eigenvector (in this case a vector of 1s) and the resulting vector normalized and again multiplied by the matrix. This process is repeated for a large number of iterations (in this case 2 000 000) until the vector remains steady at the required number of decimal places (in this case 4).

For network matrices which are not symmetric such as the movement count matrices used here, there are three different approaches for calculating centrality indices for a given node (Jacoby et al. 2012).

[1] Note that the matrix power of a matrix **A** with a non-negative integer power n is defined as the product of n copies of **A,** i.e. $\mathbf{A}^n = \underbrace{\mathbf{A}\mathbf{A}\ldots\mathbf{A}}_{n}$

1. Make the matrix symmetric by computing the sum ($\mathbf{M}+\mathbf{M}^T$, with $\mathbf{M}^T$ being the transpose of matrix **M**) or mean ($0.5*(\mathbf{M}+\mathbf{M}^T)$) of ingoing and outgoing weights for each state.

2. Compute the out-centrality of a state. Since element m_{ij} of the movement matrix **M** is the number of times a movement was made from *i* to *j*, computing the indices as outlined above for the movement matrix gives the out-centrality of state *i*.

3. Compute the in-centrality of a state. To compute the in-centrality of a state, the indices are computed as outlined above for the transpose of the movement matrix ($\mathbf{M}^T$) where m^T_{ij} is the number of times a movement was made to state *i*, from state *j*.

Since the given analysis is concerned with elucidating patterns of directed movement of sharks towards a preferred area, in-centrality measures were deemed more informative as the number of times a shark moved to an area is more indicative of a shark's preference of the area than the number of times a shark moved out of an area.

4.2.5 Empirically derived Markov chain (EDMC) analysis

The spatial network analysis described previously in this chapter, only deals with directed movements between locations, accounting for the chronological sequence of detections but not their absolute timing. While this has the advantage that time periods without detections do not need to be accounted for, it ignores significant temporal characteristics of movement patterns such as residency periods and duration of transitions between locations. In order to

include the temporal dimension of movement patterns, I employed several different variations of a Markov chain approach. Similar to the spatial network analysis, the Markov approach relies on characterising a matrix which describes the movements between states. However, for the Markov chain approach, I utilized the unique date-time stamp of each detection, computing movement count matrices for a regular, discrete timestep. To do this, I created a half-hourly, regular time series for each tagged shark, in which date-time stamps that did not have a detection associated with them were assigned to an absent state.

Movement count matrices were then computed as for the spatial network analysis, however in this case each movement occurred in a unit time step of 0.5 hours and the square matrix of movement counts contains movements from each state to itself (residency periods) as well as movements into the absent state (transition periods spent outside of the receivers range). For each sex, I constructed three different movement count matrices that deal with this absent state in different ways: we term these the simple EDMC, the spatial EDMC 1 and the spatial EDMC 2:

Simple EDMC - This is the simplest case whereby a single absent state was defined, hence whenever an animal was not detected it was considered to be in this absent state and it was possible to move from any receiver state into this absent state and vice versa.

Spatial EDMC1- Here, we resolved the absent state further into multiple spatially defined absent states based on the detections directly before and after an animal was out of detection

range. To illustrate, if an animal was detected in receiver group 2 at time *t* and then detected at receiver group 3 at time *t*+2, we know that it had to be in the area between groups 2 and 3 at time *t*+1 and the timestamp *t*+1 was assigned to state 2.3. Correspondingly, if an animal was detected at receiver group 2 at time t and then detected again at group 2 at time *t*+2 we know that it had to be either between groups 2 and 3 or between groups 2 and 1 at time *t*+1 and the timestamp *t*+1 was assigned state 2.3/2.1, a hybrid state which encapsulated the uncertainty about which of the two neighbouring states the shark could have transited into. Since the dataset contained some undetected passes through curtains, this resolution of the absent state was not always possible and for these cases we assigned a generic absent state as used in the simple EDMC.

Spatial EDMC 2 – This is a minor variant of EDMC 1 where we resolved the absent state in the same way as for the spatial EDMC 1 but we removed any undetected passes by splitting detection sequences into sub-sequences at the point of the undetected pass, hence removing the need for a generic absent state.

From these, I tallied three movement count matrices from which stochastic transition probability matrices (**T**) were constructed. This is achieved by dividing each number of transitions made from one state to another or itself by the total number of transitions made from the state:

$$t_{ij}=\Pr(\text{state}=i \rightarrow \text{state}=j)=\frac{f_{ij}}{\sum_{j=1}^{m} f_{ij}}$$

Where f_{ij} are the frequency of transitions from state *i* to state *j* amongst m possible states. Zucchini & Macdonald (2009, p21) outline how this is a conditional maximum likelihood estimator of the transition probabilities $\mathbf{T}_{ij}$ given a known starting state. Assuming the movement of sharks is a Markovian process, i.e. a process in which the probability of being in a state is only dependent on the previous state, and that probabilities are stationary, i.e. do not change with time, the transition probability matrices define the sequence of movement within the coastal area.

Analogous to the eigenvector centrality outlined above, the dominant eigenvector ($\mathbf{v}_0$) of the transition matrix (**T**) is equivalent to the row sums of the k^{th} integer power of **T**, as $k \rightarrow \infty$, where *k* is the number of timesteps. If calculated for the transition matrix transpose $\mathbf{T}^{\mathsf{T}}$, it represents the steady state of the Markov chain i.e. the probability of being in a given state, irrespective of the starting state. Eigenevctors for the transition matrices were calculated using the power method as outlined above.

4.2.6 Pattern oriented modeling (POM)

In order to determine the ability of the three types of EDMC to reproduce characteristic patterns of the shark movement process in the coastal areas, I employed pattern oriented modeling (Grimm et al. 2005, Vinatier et al. 2011). This involves simulating from an empirically estimated model and then assessing whether the simulations accord with the observed data. Simulating from a Markov chain involves probabilistically drawing states conditional on the current state using the transition matrix i.e.

$$S(t+1) \sim \text{dcat}(t_{s(t)*})$$

Where dcat() is a categorical distribution and the $t_{s(t)*}$ is the row of the transition matrix **T** corresponding to the current state *S*. I simulated 1000 movement sequences each consisting of 15000 half-hourly time steps (approximately 312 days, similar to mean length of observed detection sequences, Table 4.1) with randomly selected starting states from the transition probability matrices, calculated six ecological variables pertaining to different aspects of an animal's space-use from the simulated data and compared them to values derived from the observations. The six ecological variables were:

1) maximum movement range after 30 days

2) maximum movement range after 60 days

3) maximum movement range after 90 days

4) % of total time spent near the reserve boundaries (i.e states 3 & 4 (Fig. 4.1))

5) time after tagging to move from the Derwent to Norfolk Bay (Fig. 4.1) or vice versa

6) proportion of animals moving from the Derwent to Norfolk Bay or vice versa

For variables 1-5, simulations provided distributions which were compared to the distribution of observed values using the 2-sample Kolmogorov-Smirnov test, which determines the maximum vertical deviation between two empirical cumulative distribution functions (ECDF) with the null hypothesis that the 2 samples (simulation and observation) were drawn from the same distribution. Since distances calculated for variables 1-3 are calculated as maximum number of states visited and therefore not strictly continuous, the data contained a large number of ties (i.e. duplicate values within the data) and p-values are unreliable using the

standard implementation of the Kolmogorov-Smirnov test. Hence, p-values were estimated using bootstrapping with 10000 resamples (ks.boot() function in R package “Matching”, Sekhon, 2011), i.e. the test statistic was computed for 10000 bootstrap samples of the original data to determine the reliability of the estimated p-value.

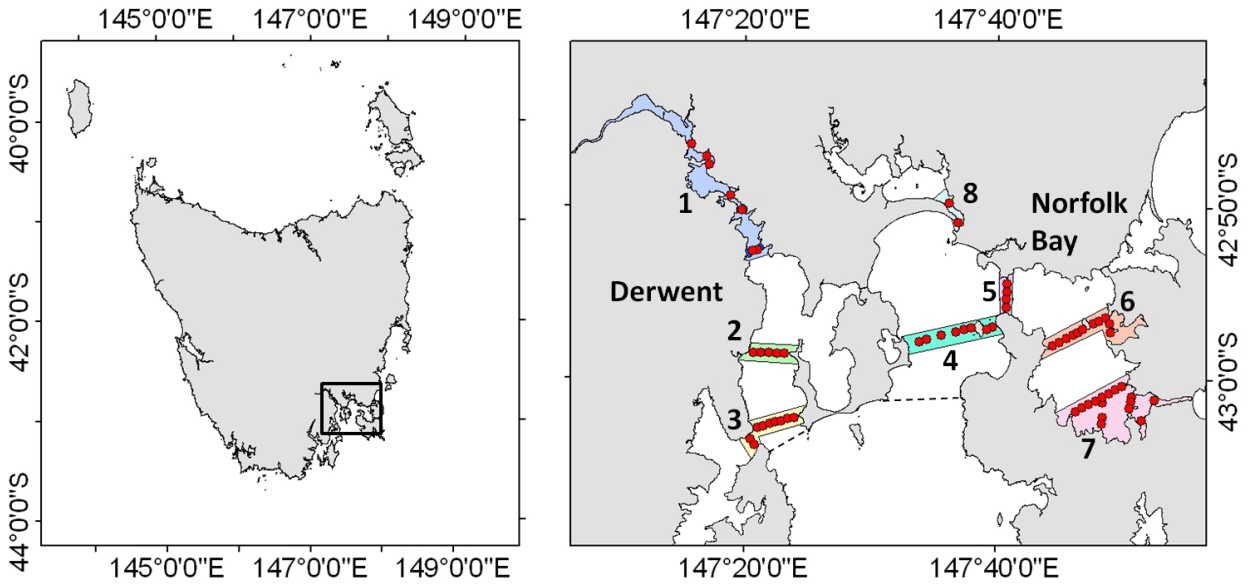


Figure 4.1 Map of the study area showing acoustic receiver locations (red dots). Black rectangle in the map of Tasmania on the left indicates extent of close-up map on the right. Dashed lines indicate shark nursery protected area boundaries. Background colours and numbers 1-8 identify receiver groupings (spatial states) used for data analyses.

4.3 Results

4.3.1 Dataset overview

A total of 29 females and 11 male broadnose sevengill sharks were tagged. Tagging of females was relatively evenly spread between Norfolk Bay and the Derwent, whereas the majority of males were tagged in Norfolk Bay (Table 4.1). However, approximately half of all females and half of all males moved between the two tagging areas, providing sufficient movement data for the two areas for each sex. All tagged male sharks were above the reported length threshold for maturity and therefore considered mature whereas 10 of the 29 tagged females were less than 210 cm long and were considered juvenile or subadult at the time of tagging. The raw dataset consisted of a total of 736911 acoustic detections at 70 receivers, covering an entire year, from November 2008 to November 2009.

Temporal and spatial aggregation reduced the raw dataset to records of half-hourly detections in 8 spatial states (Fig. 4.1) with 24571 records for female and 13976 records for male sharks. The longest detection sequence was recorded for a female shark (625 days), however, mean data series length was greater for males (Table 4.1). Percentage of half hourly time steps with detections was less than 1% for both sexes and no individual from either sex spent more than 4 days continuously within receiver range. Yet the mean of the maximum period without detections differed greatly for the sexes and was almost twice as long for males as for females. The largest number of detections of male sharks occurred in states 1 and 4, with the largest number of transitions occurring between states 4 and 5 (321 times), whereas the largest

number of detections of female sharks occurred in states 2 and 5 and the largest number of transitions occurred between states 2 and 3 (366 times) (Fig. 4.2). All states in the coastal system were visited by female sharks, whereas no male sharks were detected in state 8, resulting in a smaller mean number of states visited than for females (Table 4.1). For males, 21 undetected passes through a state were recorded, with the majority of them occurring between states 1 and 3. For females 31 undetected passes were recorded, mainly between states 1 and 3 and between states 2 and 4.

4.3.2 Social network analysis

Mean association between individuals, based on spatio-temporal co-occurrences was very low for all individuals and even more so between males and females (Table 4.2). Nevertheless, associations were not random, as the coefficient of variation was significantly higher ($p>0.025$) than in the randomized dataset. This is due to the large proportion of zero elements on the one hand, which is significantly larger than in the permuted data and a relatively highly associated group of three female sharks on the other. These three females, which were all subadults (<210 cm TL), were all detected simultaneously in state 7 over multiple sampling periods, resulting in the only SRI values above 0.1.

Lowering the temporal resolution from 0.5 to 12 hours decreased the proportion of zero elements, yet it was still significantly higher than would be expected at random. Correspondingly, mean association increased and was significantly higher than would be

expected at random between all fish, yet significantly lower between the sexes, indicating a spatio-temporal segregation between males and females (Table 4.2)

4.3.3 Spatial network analysis

Analysis of the movement network showed that both degree centrality (DC) and eigenvector centrality (EVC) of spatial states differed from the null model of random movement represented by the adjacency matrix (Fig. 4.3). While for males, which did not visit state 8 (Fig. 4.2), DC would be expected to differ from the adjacency matrix, for the female movement network, in which all adjacent nodes are connected, the two should be the same. Hence, in this case, the difference is a result of undetected passes connecting nodes in the female movement network which are not adjacent. In contrast to DC, EVC is weighted by transition frequencies and is therefore expected to differ between the adjacency matrix and the movement network if movement is non-random. This was the case for both males and females. While state 4 had the highest EVC for the adjacency matrix, states 2 and 3 had the highest EVC for males, followed by state 1 and state 6 had the highest EVC for females, followed by state 5 (Fig. 4.3).

4.3.4 Pattern oriented modeling (POM)

Pattern oriented modeling showed that the simple EDMC was an inadequate representation of coastal shark movement patterns. Using a generic absent state which is accessible from any location resulted in inflated movement rates influencing all 6 ecological indices, with distances between the observed and simulated ECDF as determined through the 2 sample Kolmogorov-Smirnov test being close to the maximum 1 in almost all cases (Tables 4.3 & 4.4). Additionally,

nearly all tracks simulated with the simple EDMC moved between the Derwent and Norfolk Bay, whereas only 46% of all tagged males and 52% of all tagged females made the movement (Table 4.5). While both spatial EDMCs performed better than the simple EDMC across all 6 indices, only spatial EDMC 2 managed to adequately reproduce movement ranges of both males and females after 30, 60 and 90 days (Fig. 4.4) with Kolmogorov-Smirnov tests showing a consistently small difference in distributions and large p-values ($p<0.05$) indicating no significant difference between observed and simulated data (Tables 4.3 & 4.4). The spatial EDMC 1, performed badly at reproducing movement ranges, primarily due to an overestimation of frequency in the higher spectrum of movement ranges for males, and an overestimation of frequencies at the lower spectrum for females. Additionally, comparison of the changes in movement range distribution between the 30, 60 and 90 day periods showed that for males spatial EDMC 1 overestimated the increase in movement range with time relative to the observed data (Fig. 4.4), whereas for females the increase in movement rate was underestimated.

Both spatial EDMC simulations performed similarly well at reproducing the proportion of time males spent near the reserve boundary, whereas, neither performed well for females for this index due to an underestimation of number of individuals that spend no or very little time near the reserve boundary (Fig. 4.5). This is also evident in the mean which is nearly twice as high as the observed value (Table 4.4). Both spatial EDMCs performed reasonably well for the time males spent near the reserve boundary as well as the time taken since tagging to make a move between the Derwent and Norfolk Bay for both sexes with no significant differences between

observed and simulated ECDFs. The proportion of individuals that make the move between Derwent and Norfolk Bay, however, was overestimated by the spatial EDMC 1 while the spatial EDMC 2 performed better, particularly for the proportion of males (Table 4.5).

Given that the spatial EDMC 2 performed well over the largest range of indices for both sexes, we used the eigenvector for its probability matrix to rank spatial states in the coastal area and compare the results to the eigenvector centrality rank from the spatial network analysis.

4.3.5 Comparison of eigenvector ranks

Eigenvector ranks for the spatial EDMC 2 varied considerably between males and females and were very different to eigenvector centrality ranks from the spatial network analysis. Both males and females were most likely to be in one of the spatially resolved absent states (summed probability for males = 0.92, for females = 0.94), expectedly so, given the low proportion of time animals spent within the receivers' range (Table 4.1). Out of the detectable states, state 1 had the highest rank for males, followed by state 4, whereas state 2 had the highest rank for females followed by state 1. In contrast to the EVC, state 2 had a relatively low rank for males and state 5 had a relatively low rank for females. States 3, 6, 7 and 8 were all at the lower end of the ranking and in the same order for males and females.

Table 4.1 Dataset overview

Sex	Number of Individuals tagged	Length of data series (days)	Number of states visited	% of total half hourly timesteps with detections	Maximum time without detections (days)	Max duration without gaps in detections (hours)
Males	4 tagged in the Derwent 7 tagged in Norfolk Bay	Mean=317.2 (range=6.3-477.9, sd=181.6)	Mean=4.55 (range=3-7, sd=1.44)	Mean=0.4% (range=0.2-1%, sd=0.2%)	Mean=155.6 (range=2.3-263.9, sd=113.8)	Mean=18.1 (range=1-77, sd=20.2)
Females	14 tagged in the Derwent 15 tagged in Norfolk Bay	Mean=269.3 (range=8.6-625.1, sd=181.3)	Mean=5.10 (range=2-8, sd=1.97)	Mean=0.4% (range=0.02-1.5%, sd=0.3%)	Mean=76.4 (range=2.0-216.7, sd=64.0)	Mean=16.6 (range=1-64, sd=12.6)

Table 4.2 Comparison of proportion of SRI elements of value zero, mean SRI and coefficient of variation (C.V.) of the SRI for the real association data and those obtained from 20000 permutations. p-values for the rejection of the null hypothesis of no difference between observed and random values are given. Grey shading indicates significant results i.e. p-values <0.025. Values are presented for both 0.5 and 12 hour sampling periods and for all individuals as well as for associations between males and females only.

	0.5 hourly		**12 hourly**	
	All fish	Between sexes	All fish	Between sexes
Real proportion of zero elements	0.5718	0.6113	0.4769	0.5204
Permuted proportion of zero elements	0.4485	0.5952	0.327	0.4188
p-value	<0.025	<0.025	<0.025	<0.025
Real mean	0.0052	0.0031	0.0219	0.0164
Permuted mean	0.0052	0.0031	0.0217	0.0166
p-value	>0.025	>0.025	<0.025	<0.025
Real C.V.	2.5894	2.4261	2.1399	1.1644
Permuted C.V.	2.3693	2.4154	1.6023	1.1885
p-value	<0.025	<0.025	<0.025	>0.025

Table 4.3 Results for pattern-oriented modeling of 5 pertinent ecological indices of space-use for male sharks. Means are given for observed data, the simple EDMC and spatial EDMC 1 and 2. Kolmogorov-Smirnov distances between observed and simulated ECDFs are presented as well as significance levels for the rejection of the null hypothesis of no difference between observed and simulated ECDFs. For means, standard deviations are given in brackets. Grey shading indicates results with no significant difference between observed and simulated data ($p>0.05$).

Indices	Mean Observed Data	Mean simple EDMC	Kolmogorov-Smirnov	Mean spatial EDMC 1	Kolmogorov-Smirnov	Mean spatial EDMC 2	Kolmogorov-Smirnov
Movement range – 30 days	1.909 (0.831)	6 (0)	1 ($p<0.025$)	2.697 (1.050)	0.272 ($p>0.05$)	1.662 (0.919)	0.098 ($p>0.05$)
Movement range - 60 days	2.636 (1.120)	6 (0)	1 ($p<0.025$)	3.411 (1.202)	0.350 ($p<0.025$)	2.175 (0.823)	0.173 ($p>0.05$)
Movement range – 90 days	2.818 (0.982)	6 (0)	1 ($p<0.025$)	3.917 (1.288)	0.367 ($p<0.025$)	2.492 (0.815)	0.139 ($p>0.05$)
Proportion of time spent near reserve boundary	3.827 (6.198)	3.434 (0.226)	0.631 ($p<0.025$)	3.707 (2.221)	0.362 ($p>0.05$)	3.585 (1.355)	0.361 ($p>0.05$)
Time to move between Derwent and Norfolk Bay	147.404 (155.581)	0.412 (0.376)	1 ($p<0.025$)	101.181 (79.402)	0.355 ($p>0.05$)	153 (82.087)	0.395 ($p>0.05$)

Table 4.4 Results for pattern-oriented modeling of 5 pertinent ecological indices of space-use for female sharks. Means are given for observed data, the simple EDMC and spatial EDMC 1 and 2. Kolmogorov-Smirnov distances between observed and simulated ECDFs are presented as well as significance levels for the rejection of the null hypothesis of no difference between observed and simulated ECDFs. For means, standard deviations are given in brackets. Grey shading indicates results with no significant difference between observed and simulated data ($p>0.05$).

Indices	Mean Observed Data	Mean simple EDMC	Kolmogorov-Smirnov	Mean spatial EDMC 1	Kolmogorov-Smirnov	Mean spatial EDMC 2	Kolmogorov-Smirnov
Movement range – 30 days	2.103 (1.175)	6 (0)	1 ($p<0.025$)	1.488 (0.900)	0.312 ($p<0.025$)	1.724 (0.788)	0.167 ($p>0.05$)
Movement range - 60 days	2.586 (1.150)	6 (0)	0.966 ($p<0.025$)	2.146 (1.147)	0.292 ($p<0.025$)	2.256 (0.952)	0.147 ($p>0.05$)
Movement range – 90 days	3.069 (1.387)	6 (0)	0.931 ($p<0.025$)	2.568 (1.313)	0.293 ($p<0.025$)	2.635 (1.038)	0.164 ($p>0.05$)
Proportion of time spent near reserve boundary	0.827 (1.215)	1.719 (0.176)	0.862 ($p<0.025$)	1.434 (0.814)	0.546 ($p<0.025$)	1.611 (0.657)	0.617 ($p<0.025$)
Time to move between Derwent and Norfolk Bay	116.510 (97.765)	0.802 (0.760)	0.936 ($p<0.025$)	126.236 (89.368)	0.168 ($p>0.05$)	138.578 (80.694)	0.245 ($p>0.05$)

Table 4.5 Proportion of male and female sharks moving between the Derwent and Norfolk Bay for the observed data, simple EDMC and spatial EDMCs 1 and 2. Grey shading indicates the EDMC with values closest to the observed proportion.

	Observed data	Simple EDMC	Spatial EDMC 1	Spatial EDMC 2
Proportion of males moving between the Derwent and Norfolk Bay	0.46	1.00	0.90	0.35
Proportion of females moving between the Derwent and Norfolk Bay	0.52	1.00	0.71	0.68

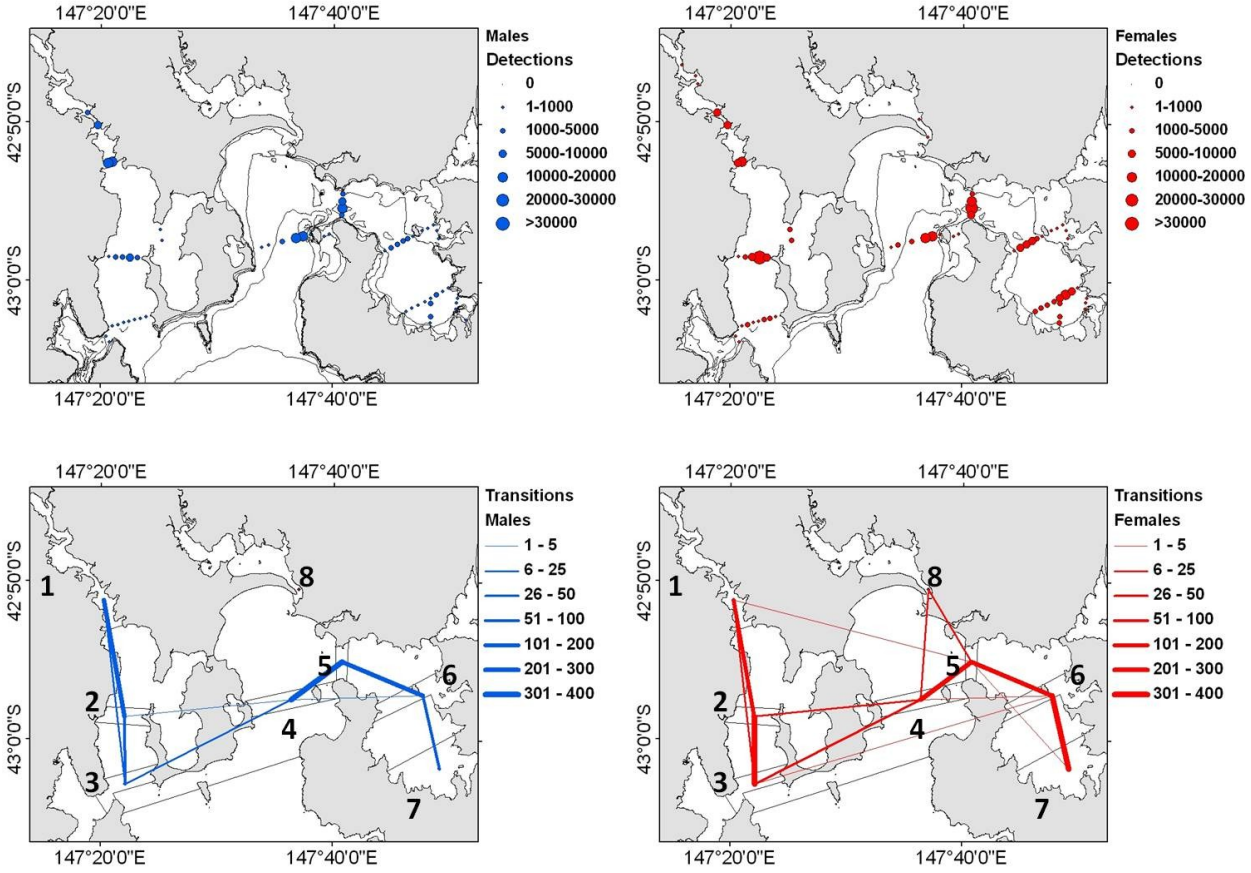


Figure 4.2 Detection (top panel) and transition (bottom panel) frequencies for male (blue) and female (red) broadnose sevengill sharks. Numbers indicate spatial states (i.e. receiver groups).

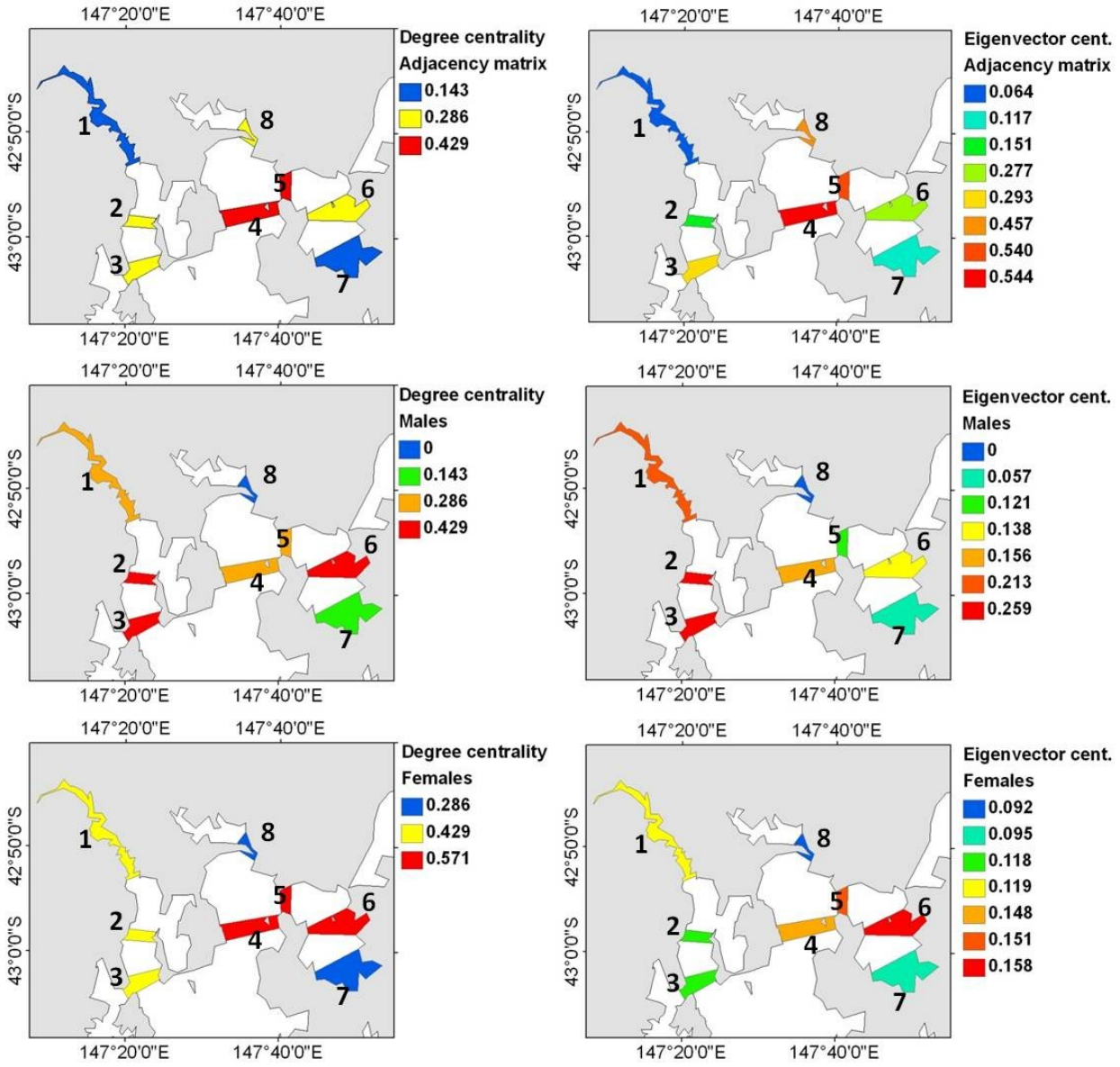


Figure 4.3 Degree centrality (left panel) and eigenvector centrality (right panel) ranks computed for the adjacency matrix and the matrix of between-state transition frequencies for male and female broadnose sevengill sharks. Numbers show absolute centrality values, colours indicate relative ranks of the spatial states.

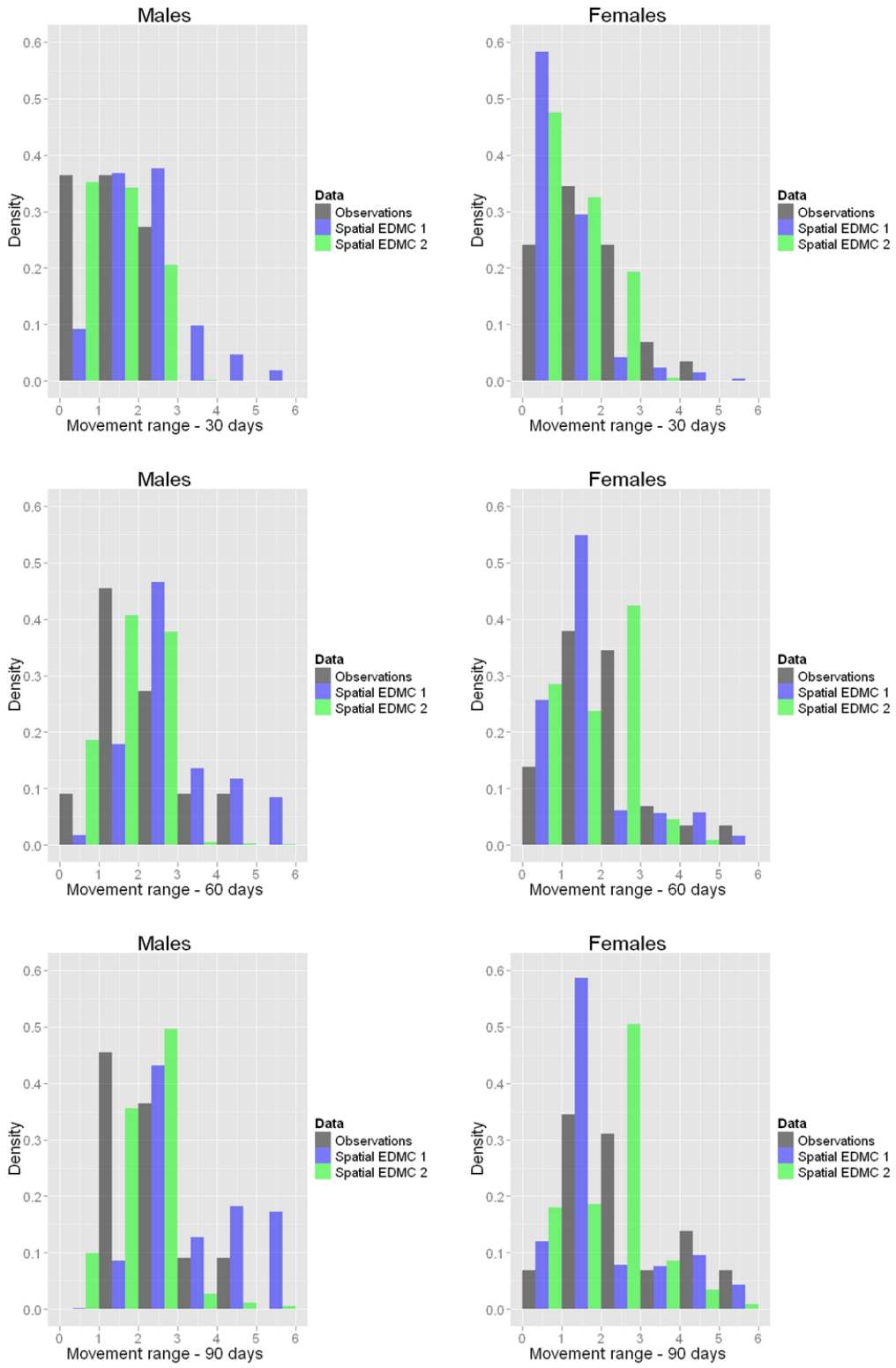


Figure 4.4 Density distribution of movement range (in number of spatial states visited) after 30 (top), 60 (centre) and 90 (bottom) days since tagging for observed data and simulations from spatial EDMCs 1 and 2 for male (left panel) and female (right panel) broadnose sevengill sharks.

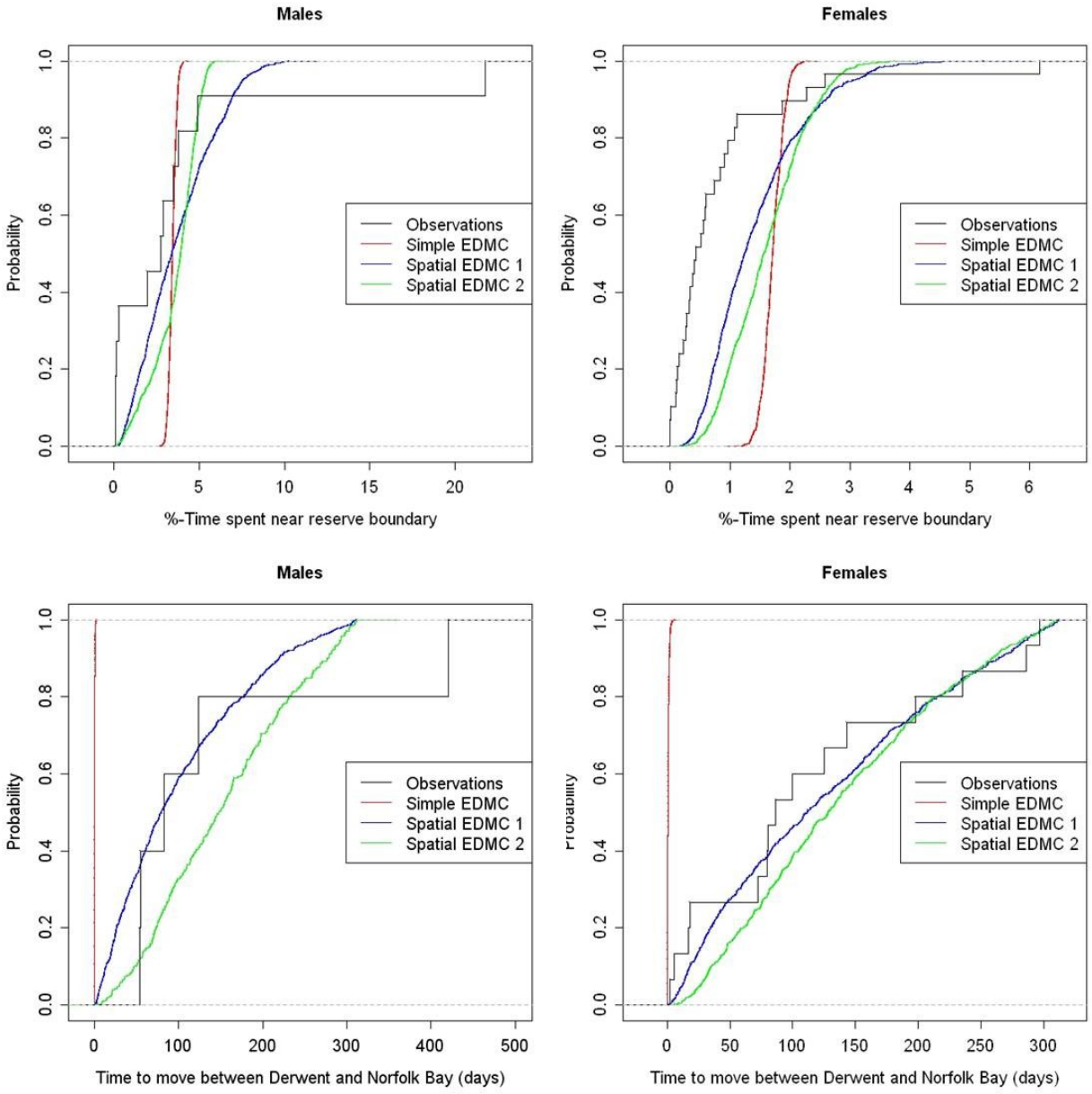


Figure 4.5 Cumulative empirical distribution functions (CEDFs) for percent of time spent near the shark nursery area boundaries (spatial states 3 & 4) (top) and time taken since tagging to move from the Derwent to Norfolk Bay or vice versa (bottom) for the observed data, simple EDMC and spatial EDMCs 1 and 2 for male (left panel) and female (right panel) broadnose sevengill sharks.

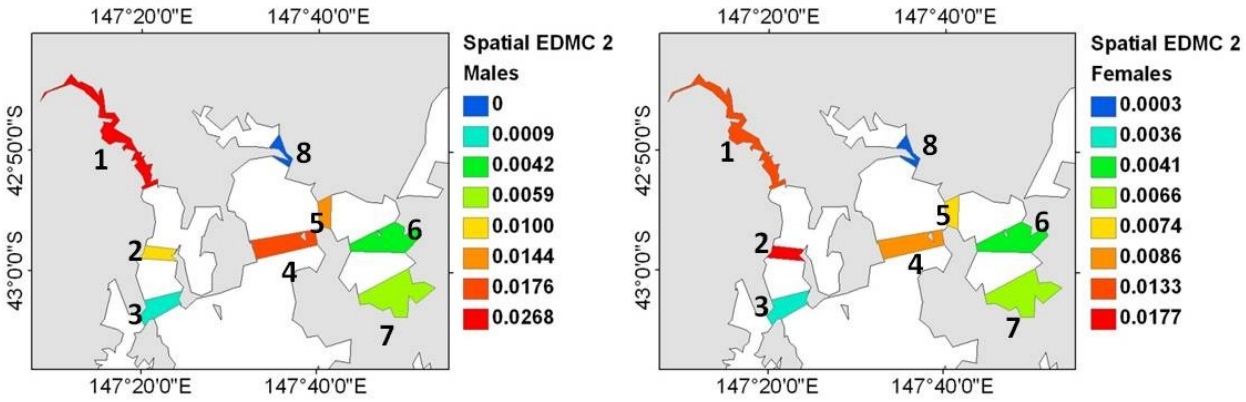


Figure 4.6 Ranks of spatial states from the dominant eigenvector of the transition probability matrix for spatial EDMC 2 for male (left) and female (right) broadnose sevengill sharks. Numbers show absolute eigenvector values, colours indicate relative ranks of the spatial states.

4.4 Discussion

In this study of movements of the broadnose sevengill shark from automated acoustic telemetry, a combination of social network analysis, spatial network analysis and stochastic modeling revealed spatial segregation of the sexes during the sharks' seasonal residency in the coastal areas of south-east Tasmania. Male and female sharks showed little spatio-temporal overlap in their use of coastal areas and displayed sex-specific preferences of different sites within the study area.

Social network analysis of spatio-temporal co-occurrences showed that overall there was low spatial overlap between individuals at a fine temporal resolution. The exception to this was a group of 3 subadult females, which were continuously detected at the same group of receivers within the same half-hour over a 2 month period. It is unclear whether broadnose sevengills routinely aggregate in groups and the spatial resolution in this study was too coarse to shed further light on the subject, as it was not possible to distinguish between shared patterns in space-use and social interactions. However, aggregating behaviour has been observed in the juveniles and subadults of a number of shark species (e.g. blacktip shark, Heupel & Simpfendorfer 2005, lemon shark, Morrissey & Gruber 1993) and is generally attributed to predator avoidance (Jacoby et al. 2011). Another explanation for possible grouping behaviour is socially facilitated hunting, which has been reported for this species in South African waters (Ebert 1991), where groups of sharks co-operated to strike larger prey items such as fur seals. While there are a few examples of such social interactions of sharks (e.g. scalloped

hammerhead, Klimley 1985) and the brain-mass to body-mass ratios of sharks suggest they are capable of complex social behaviours (Myrberg Jr & Gruber 1974, Sims 2005), with a few exceptions (Jacoby et al. 2010, Mourier et al. 2011) little is known about the mechanisms and patterns of social interactions in sharks. However, the development of animal-borne imaging devices (Heithaus et al. 2001, Skomal et al. 2007) and novel acoustic tags which can record the presence of other tagged individuals within a given radius (Holland et al. 2009, Guttridge et al. 2010) at fine spatial scales is likely to facilitate the study of the interplay between individual movement and social interactions in the near future (Jacoby et al. 2011).

At a coarser temporal scale of 12 hourly sampling periods, the social network analysis in this study showed a greater frequency of co-occurrences of tagged sharks than at the fine temporal scale, however, co-occurrences of male and female sharks were significantly less frequent than would be expected at random, indicating the likelihood of sexual segregation for this species, at least within coastal areas. This is in contrast to the findings of resource overlap from the same dataset by (Barnett et al. 2011) who suggested a high degree of spatial overlap between males and females based on the calculation of Pianka's Index (Pianka 1974) for frequencies of detections at individual receivers. The reason for the discrepancy between the two methods is that in contrast to the social network analysis, Pianka's Index does not include a temporal dimension (i.e. the timing of presence in a state). Since the resources exploited by broadnose sevengill sharks are generally highly mobile prey species (Barnett et al. 2010a) whose distribution is likely to be variable in both space and time, methods such as social network

analysis, which explicitly include the temporal aspect of co-occurrence, are likely to provide a more complete picture of the degree of resource overlap from the acoustic telemetry data. Both spatial network analysis and Markov chain analysis showed that the spatial segregation of the sexes was due to sex-specific preferences of different sites within the study area, resulting in differences in space-use patterns. Spatial segregation of the sexes is a common phenomenon in sharks (see Sims 2005, for review) and has been reported for numerous species (e.g. great white shark, Robbins 2007, shortfin mako, Mucientes et al. 2009, dogfish, Sims et al. 2001). Three main theories adapted from terrestrial mammal ecology have been proposed as the drivers behind sexual segregation in sharks (Sims 2005):

1) The forage selection hypothesis
2) The reproductive strategy hypothesis
3) The social factors hypothesis

The forage selection hypothesis (Ruckstuhl & Neuhaus 2002) states that sexual segregation is due to differences in energy expenditure and hence energy requirements caused by sexual dimorphism. In many ovoviviparous shark species such as the broadnose sevengill shark, females grow larger than males as a result of their reproductive requirements, potentially resulting in the selection of different foraging habitats (Klimley 1987). This was suggested as one of the possible reasons for the sex-specific differences in the large-scale movement behaviour of sevengill sharks described in chapter 3. During the sharks' residency in the coastal areas, however, Barnett et al. (2010a) found high dietary overlap between sharks caught at different locations and the habitat in the Derwent and Norfolk Bay is relatively uniform,

indicating that factors other than sex-specific foraging strategies might be driving spatial segregation.

The reproductive strategy hypothesis (Ruckstuhl & Neuhaus 2002) states that the females of a species are more likely to prioritize predator avoidance over forage quality to ensure reproductive success. However, since the only predator of sevengill sharks in the coastal areas are conspecifics (Barnett et al. 2010a) and females grow larger than males, predator avoidance is unlikely to determine the space-use of female sevengill sharks.

The social factors hypothesis (Main et al. 1996) states that spatial segregation is the result of aggressive behaviour of one sex to another. Aggressive mating behaviour is common in many shark species (Sims et al. 2001, Litvinov 2006, Mucientes et al. 2009) with mating attempts often resulting in substantial injuries to the body and fins of the female (Carrier et al. 1994). Barnett et al. (2011) reported the absence of fresh mating injuries on females caught in the coastal areas in summer and suggested that sevengill sharks might form mating aggregations in the lower part of the Derwent, based on the fact that both males and females aggregated in this area in late autumn, prior to leaving the coastal embayment. If this is the case, females may be avoiding males prior to these mating events to prevent costly courtship or copulation attempts.

Although spatial network analysis and Markov chain analysis both indicated sex-specific differences in space-use, the two methods differed considerably in their identification of preferred areas for male and female sharks. This is most likely due to the fact that spatial

network analysis does not account for repeated detections at a receiver (residency periods) or time spent outside of the receivers' range (transition times), which was overwhelmingly large in the array design used in this study. The first applications of spatial network analysis to animal telemetry data determined the importance of roosting trees in movement networks of bats (Rhodes et al. 2006, Fortuna et al. 2009). Since it is known that bats spend the daytime roosting and the night-time moving between trees, in this case, both residency periods and transition times were known and constant and the inclusion of a temporal dimension was not required. Moreover, inclusion of a temporal element is generally not required when the temporal dimension does not affect the ecological process in question. For determining the spatial dimension of disease transmission (Godfrey et al. 2009) or encounter rates between fish schools (Stehfest et al. 2013) for example, network analysis provides a simple tool for condensing transition patterns between locations into easily digestible metrics. When elucidating general movement patterns from acoustic telemetry data, however, results are likely to be biased by the exclusion of timing of detections and transitions.

The magnitude of this bias is dependent on both the movement behaviour of the study species and the design of the acoustic array. Jacoby et al. (2012), who first proposed the spatial network analysis of automated acoustic tracking data, analysed the movement of two highly mobile species of sharks in a gridded array with high receiver density. In this case residency periods as well as periods spent outside of the receiver range are likely to be small relative to between-receiver transition frequencies and spatial network analysis will provide an adequate representation of movement patterns. Moreover, unlike the curtain array used in this study, a

gridded array does not allow the straightforward resolution of the absent state into multiple spatially defined states. As the pattern oriented modeling approach in this study showed, the use of a uniform absent state leads to a gross exaggeration of movement rates. Hence for the type of array where the absent state cannot be resolved, such as the gridded array used by Jacoby et al. (2012), the spatial network analysis might be preferable over the Markov chain analyses proposed in this chapter. For the array design and study species of this chapter, however, which resulted in a dataset with large amounts of time spent outside of the receivers' range and continuous residency periods of up to 77 hours, the Markov chain analysis is likely to be a better representation of the movement patterns of broadnose sevengill sharks.

This was confirmed by the pattern oriented modeling approach, which showed that despite its simplicity, the Markov chain model adequately captured the majority of characteristics of the coastal shark movement. The only movement/ecological index that the Markov chain model was not able to adequately approximate was the residency of both males and females near the protected area boundary. This highlights one of the main limitations of the method. Both the lower and upper ends of the spectrum were underestimated for this index, suggesting high individual differences in residency patterns which were not captured by my simple model. Accounting for individual variability is statistically challenging and methods for accounting for individual differences within Markovian models are still in development (e.g. Ford et al. 2012). Nevertheless, the model was useful to identify hypotheses for future research as the variability in residence time in a given area hints at the possibility of individual home ranging behaviour

which has been reported for a number of other coastal shark species (see Speed et al. 2010, for review).

The other main limitation of my approach is the inability to fully resolve the absent state into multiple discrete spatial states. As the Markov chain analysis identified, sharks had an overwhelmingly large probability of being outside of the receivers' range, which is one of the drawbacks of curtain arrays, where the detection effort is highly focused in a limited number of areas. The resolution of the absent state could be achieved by producing a full Markov movement model, in which movement probabilities for absent states are determined using maximum likelihood or Bayesian Markov-chain Monte Carlo estimation (e.g. Deriso et al. 1991, Johnson et al. 2004, Eveson et al. 2009). Such a model could also resolve the absent state in a gridded array as used by (Jacoby et al. 2012) and could include non-stationary transition probabilities, accounting for seasonal shifts in space-use, which the simple Markov chain cannot. However, for large data sets these models are computationally demanding and can be difficult to construct for non-specialists.

The method proposed here on the other hand is comparatively simple and due to its prominence as the foundation of Google's search algorithm (Brin & Page 1998) a plethora of information on its concepts and computation are available (e.g. Langville & Meyer 2005, Franceschet 2011); and despite its simplicity it performed surprisingly well in determining sex-specific differences in space-use and identifying preferred areas for male and female broadnose sevengill sharks. Unfortunately the design of the curtain array in this study did not allow the

identification of mechanisms that drive the preference of one area over another, as receivers were not placed in ecologically meaningful locations. The application of the Markov chain analysis to data from an array where receiver placement is stratified by habitat type, however, would allow the explicit testing of habitat preference hypotheses, which has been identified as one of the major challenges in deepening our understanding of the movement ecology of sharks (Sims 2009).

Understanding the space-use patterns of animals in the context of the habitats they encounter and their interactions with conspecifics is one of the fundamental challenges of movement ecology (Nathan et al. 2008). Adopting methods widely used in the social sciences (Krause et al. 2009) and the ranking of webpages in internet search engines (Brin & Page 1998) I managed to gain novel insights into the space-use patterns of male and female broadnose sevengill sharks from an acoustic tracking dataset that had been analysed previously using standard statistical techniques (Barnett et al. 2011, Barnett & Semmens 2012). My analysis identified spatial segregation between the sexes, possibly due to male avoidance behaviour by females, resulting in distinct space-use patterns for each sex. In addition to the ecological findings, this study highlights the great potential of adopting methods from other scientific disciplines to maximise the information gained from acoustic tracking data and advance our understanding of a species' movement ecology.

Chapter 5 - General discussion

The aim of this thesis was to develop novel methods for quantifying the movement behaviour of two species of highly mobile, free-ranging fish using automated acoustic tracking data and improve our understanding of the animals' space-use. This work has been situated in the context of the recently formulated unifying movement ecology paradigm (Nathan et al. 2008) which states that movement patterns emerge through the interplay of an individual's internal state and external factors, which can vary over a large range of spatial and temporal scales during an animal's total lifetime movement track (Nathan et al. 2008).

The methods I developed aim to determine the link between movement patterns and two types of external factors: the interactions with conspecifics (Chapters 2 & 4) through aggregating behaviour and the influence of habitat (Chapter 4). As regards the influence of habitat, I attempted to determine movement patterns at two different scales in order to integrate different segments of an animal's lifetime track: large-scale seasonal migratory movement (Chapter 3) and local-scale movement within the animals' seasonal coastal residency (Chapter 4). The two species chosen for this thesis were the yellowfin tuna *Thunnus albacores* (Chapter 2) and the broadnose sevengill shark *Notorynchus cepedianus* (Chapters 3 & 4).

The acoustic tracking data for both species had been analysed previously using standard statistical techniques (Dagorn et al. 2007, Barnett et al. 2011, Barnett & Semmens 2012).

Several recent reviews have lamented the lag between the rapid technological advance in movement ecological research in general (Cooke et al. 2004) and in acoustic telemetry specifically (Heupel et al. 2006, Sims 2009) and the relatively slow development of quantitative methods for analysing the vast amounts of data collected . Hence my goal was to expand our insight into the movement ecology of the two study species through the application of novel analytical methods adapted from other fields of science.

5.1 Summary and implications of ecological findings

5.1.1 Yellowfin tuna (Thunnus albacores)

My analysis of the timing of detections of acoustically tagged yellowfin tuna at fish aggregation devices (FADs) using methods adopted from social and spatial network analysis revealed that the frequency and temporal dynamics of spatio-temporal associations between individuals showed considerable variability between the two study years. These differences were most likely due to a larger percentage of fish exhibiting between-FAD movement in one of the years, increasing the probability of encountering fish tagged at other FADs, potentially causing the threefold increase in the speed of association decay. This means that the FAD array was at a sufficient density to facilitate between-FAD movement, potentially leading to greater mixing between schools and lower school cohesion.

In order to investigate this further, similar analyses to the ones employed in this thesis could be applied to data from FAD arrays with varying degrees of FAD density as well as comparative

studies of school size in different FAD arrays to determine whether FAD density has an impact on tuna school size, as a modelling study has suggested (Dagorn & Fréon 1999). In other species, an increased exchange of individuals between schools has been shown to cause increased disease transmission and disrupt natural behavioural processes but also facilitate the transfer of information and social learning (Croft et al. 2003). To determine the impact lowered aggregation cohesion might have on the ecology of tuna, knowledge of the evolutionary or ecological advantage of the aggregating behaviour of tuna is required, which has eluded scientists thus far (Fréon & Dagorn 2000, Castro et al. 2001). One of the main proposed hypotheses and the one most strongly influenced by the impact of FADs on school cohesion is the meeting point hypothesis which states that tuna aggregate at floating objects to increase encounter rates with conspecifics and increase school size (Fréon & Dagorn 2000). Further studies on tuna, similar to the one carried out on bigeye scad, where fish were captured, held in tanks to facilitate the formation of social bonds, tagged with acoustic tags and then released near FADs equipped with acoustic receivers (Soria et al. 2009) could shed light on whether this hypothesis holds true for tuna. Additionally, the deployment of pop-up satellite archival tags (PSATs) on acoustically tagged tuna could determine whether tuna that are strongly associated at a FAD share common large-scale movement patterns after leaving the FAD. While this would be expensive due to the large number of tags required, recent multi-tag studies with large sample sizes have shown that it is not impossible (Block et al. 2011).

5.1.2 Broadnose sevengill shark (Notorynchus cepedianus)

For a species such as tuna, which inhabits a relatively homogeneous habitat and spends its entire lifetime movement track in the company of others, interactions with conspecifics and the existence of social bonds are likely to exert considerable influence on an individual's movement ecology. For species such as sharks, which are often solitary or form temporary shoals or aggregations during only parts of their lifetime movement tracks (e.g. Heupel & Simpfendorfer 2005, Klimley 1985), understanding how the animals interact with their environment is likely to hold the key to understanding their movement ecology.

My study of broadnose sevengill shark movement at two different spatial scales using PSATs and automated acoustic telemetry showed sex-specific differences in habitat preferences, both in the species' seasonal migration and coastal space-use. Males tagged with PSATs left the coastal areas of south-eastern Tasmania between mid-May and the end of June to move northwards into warmer waters, covering minimum distances of up to 880 km. Some of the females remained in the coastal system for the entire winter, while others left the coastal areas and moved into deeper waters offshore apparently without making similar long range movement to the males.

During their residency in the coastal areas in the summer months, there was overall low spatio-temporal overlap between individuals and segregation between males and females was evident, with the sexes displaying a preference for different parts of the coastal study area. The sex-specific differences in seasonal migration were consistent with the sharks' movements

being driven by either resource partitioning, caused by the greater energy demands of females, or the difference in reproductive requirements of males and females. Spatial segregation of the sexes in the coastal area on the other hand was hypothesized to be due to female avoidance behaviour which would prevent costly courtship or copulation attempts. These are known to be aggressive in many shark species (Sims et al. 2001, Litvinov 2006, Mucientes et al. 2009), often resulting in substantial injuries for the female (Carrier et al. 1994).

While the PSAT data provided new insight into the vertical movement behaviour of broadnose sevengill sharks, integration of horizontal movement data at the two different spatial scales was hindered by the unsatisfactory reconstruction of large-scale movement tracks from the PSAT geolocation data. Neither of the two movement studies managed to shed light on the reproductive ecology of the population of broadnose sevengill sharks and its link to movement behaviour. Both mating and natal sites are still unknown and further research will be required to uncover their location as they are likely to be important focal areas for conservation measures for the species (Heupel et al. 2007).

What the studies did show is that males and females are likely to be exposed to different degrees of fishing pressure which may cause differential exploitation of the sexes, as has been suggested for the shortfin mako *Isurus oxyrinchus* in the South Pacific (Mucientes et al. 2009). Hence, including the knowledge on the sex-specific differences in movement ecology gained in this thesis will be crucial for the success of any future management or conservation measures.

5.2 Methodological advances and future directions

5.2.1 Network analysis

In this thesis, I demonstrated two different types of application of network theory to automated acoustic telemetry data: Social network analysis and spatial network analysis. For the social network analysis, I adopted Whitehead's (2008) index for the quantification of social associations to quantify the frequency of spatially and temporally explicit co-occurrences of tagged individuals and its evolution over time. The great flexibility of defining co-occurrences in space (group definition) and time (sampling period definition) means that the methodology is applicable to a wide range of research questions and the ecological interpretation of the association index varies with the group definition and sampling period chosen. Fine spatial and temporal scales will allow the identification of movement synchronicity in group living animals in both space and time if the necessary data is available. Currently, this is often done by determining the temporal synchronicity of movement parameters such as speed or movement angle through time-series decomposition (Polansky et al. 2010, Polansky & Wittemyer 2011), ignoring the spatial dimension of movement data.

At coarser spatial and temporal scales, network analysis could be used to calculate a temporally explicit index of home range or space-use overlap. Currently used indices of home range overlap are generally purely spatial (e.g. Dillon & Kelly 2008, Schuttler et al. 2012), however, if ecological factors such as carrying capacity of an area, antagonistic encounters, information exchange or disease transmission are to be considered, quantifying the simultaneous nature of the space-use overlap is essential. If a group definition is chosen to represent a specific

resource, network analysis can be used to calculate the degree of resource overlap, once again providing an advantage over traditional indices (e.g. Pianka's index, Barnett et al. 2012a) by including the temporal dimension which can be tailored to the temporal variability of the resource in question.

In the case of chapter 2 of this thesis, the spatial resolution of the data allowed us to quantify the frequency and stability of associations at the level of FAD aggregations and identify possible links to between-FAD movements. To identify the direct influence of social associations and grouping behaviour on individual movement, data at a higher spatial resolution than automated acoustic telemetry can currently provide is required. One of the most exciting new technological advances in acoustic telemetry is the development of inter-animal acoustic telemetry (Holland et al. 2009, Guttridge et al. 2010) where tags are able to record when another tagged animal is within a specified radius. Similar technologies are already available for terrestrial applications (e.g. Robert et al 2012a) and have been used to determine individual contact rates both within and between species (Boehm et al. 2009). The type of data these tags can collect will allow the application of movement models for group living animals that account for social associations (Bode et al. 2011) or aggregating behaviour (Turchin 1997), improving our understanding of the link between movement and individual interactions as identified in the movement ecology paradigm (Nathan et al. 2008).

For the spatial network analysis, I followed the approach first proposed for the analysis of acoustic telemetry data by Jacoby et al. (2012), where a movement network between spatial

locations is constructed based on the frequency of directed animal movements. While the method was an easily computable and interpretable way of identifying FADs with high encounter rates between schools of tuna in chapter 2, I found it to give an incomplete representation of coastal space-use patterns of the broadnose sevengill shark in chapter 4. Since spatial network analysis does not account for transition or residency periods, it is only adequate in cases where these periods are short enough to be negligible (Jacoby et al. 2011), irrelevant for the ecological hypothesis in question (Stehfest et al. 2013) or constant and known (Rhodes et al. 2006, Fortuna et al. 2009).

5.2.2 Markov chain analysis

Standard methods for quantifying movement patterns from acoustic telemetry data generally rely heavily on the frequency of detections at individual receivers (Heupel et al. 2006), ignoring the sequencing of detections at different receivers. The method of spatial network analysis discussed above only uses the sequencing of detections at receivers and ignores the frequency of detections. I attempted to include both aspects of acoustic telemetry data by applying concepts from stochastic modelling. These concepts have a very wide application in operations research and statistics (for example they are prominently employed as the basis of the Google search engine (Brin & Page 1998)). I therefore constructed a discrete-time, stationary Markov chain movement model, which, considering its simplicity provided a surprisingly adequate representation of sex-specific coastal movement patterns of the broadnose sevengill shark. It allowed me to assign a rank of preference to parts of a coastal area based on the steady state of the Markov chain, similar to the ranking of webpages in a Google search.

The main limitation of the model I constructed was that it did not go beyond detection frequency and sequencing to include the third aspect of acoustic tracking data: The time spent outside of the receivers' range between detections. In cases such as the acoustic tracking data from tuna around FADs in chapter 2, where areas with high detection probability (the FADs) and those with 0 detection probability (the open ocean) form separate ecological entities this aspect is of little importance. For the acoustic tracking data from the broadnose sevengill sharks, however, the areas covered by the receivers' detection range are neither more significant nor likely to be ecologically different from areas without receivers. Hence, in this case any analysis of space-use patterns that cannot infer information on areas without receiver coverage remains incomplete.

In a more complex Markov model, transition probabilities could be determined for areas without receivers using maximum likelihood (e.g. Davison 2003, chapter 6) or Bayesian estimation (Clark 2007), if the adjacency matrix, i.e. the matrix defining which transitions between states are possible is suitably defined (e.g. Deriso et al. 1991). This has been done extensively at relatively coarse spatial and temporal scales to model the large-scale movement patterns of commercially exploited marine species such as shrimp (Grant et al. 1991), sablefish (Heifetz & Fujioka 1991) and tuna (Deriso et al. 1991, Eveson et al. 2009) and at very fine scales to model the movement of fish relative to the entrance of a sluiceway from sonar data (Johnson et al. 2004). Yet, thus far the application of such a model to automated telemetry data has been limited (Steel et al. 2001).

If this type of model is to be applied to acoustic telemetry data, its requirements should be considered early on in the array design process. For the analysis of movement in and out of a reserve, the curtain design used to collect the data on sevengill sharks is highly effective (Barnett et al. 2011) and having a highly focused detection probability of close to 100% at significant locations such as reserve boundaries is desirable. For the statistical estimation of transition probabilities in a Markov chain on the other hand such a patchy distribution of detection probabilities can be problematic. A more uniform spread of detection effort as implemented in a grid type array (Heupel et al. 2006) might be preferable. However, it would necessitate the estimation (either within the model or using ancillary experimental data) of detection probability parameters in the model, analogous to the estimation of recapture probability in the application of the method to mark-recapture data (Eveson et al. 2009). In a gridded array, receiver placement could also be stratified by habitat type and environmental parameters characterizing the habitat included in the model as covariates of the attractiveness of a spatial state (Vinatier et al. 2011). This would allow the explicit testing of habitat preference hypotheses, and improve our understanding of how free-ranging marine fish interact with their environment.

The two major reviews of biotelemetry published in the late 1980s predicted a quantum leap in our understanding of how animals interact with each other and their environment for the near future, due to the accelerated technological advances in the field (Cooke et al. 2004). While a number of groundbreaking studies have employed novel instruments to gain hitherto unattainable insight into the behaviour of free-ranging animals in their natural environment,

the full potential of the technology is yet to be exploited due to a limited range of quantitative methods for the analysis of the collected data. This thesis has not only provided new insight into the behavioral ecology of two free-ranging marine fish of great ecosystem importance, it has also provided a way forward for the quantitative analysis of acoustic telemetry data, in the hope of enhancing the capability of this rapidly evolving technology to assist in navigating the uncharted waters of movement ecology that lay ahead for future studies.

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Chapter 7 - Appendix I

Paper from chapter 2, published in *Animal Behaviour*

Stehfest, K.M., Patterson, T.A., Dagorn, L., Holland, K.N., Itano, D. & Semmens, J.M. 2013. Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean. *Animal Behaviour*, **85**, 839-848.